Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the soft-shell clam, *Mya arenaria* L., at several spatial scales

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Abstract

Predation appears to be the single most important biotic factor regulating populations of bivalves in estuarine and coastal soft sediments. However, the relative roles of predation and intraspecific competition are rarely investigated simultaneously over different spatial scales, making generalities about these mechanisms difficult. Using juveniles of the soft-shell clam, *Mya arenaria* (initial mean shell length [SL] ± 95% CI = 12.4 ± 0.13 mm), I tested the interactive effects of predator deterrence and intraspecific density (660 vs. 1320 individuals m^{-2}) on growth and survival responses over a 185-day period from May to November 2003 at spatial scales that spanned four orders of magnitude: embayments, sites within embayments, tidal gradients, and blocks that were 10,000's, 1000's, 100's, and 5 m apart, respectively. Replicate field experiments were conducted from May to November 2003 at the upper and lower tidal heights at each of two intertidal mud flats (sites) within each of two embayments (Passamaquoddy Bay [PB] and Cobscook Bay [CB]) in eastern Maine.

Mean survival, relative growth, and the abundance of wild recruits each varied significantly over all spatial scales. Predation was the most important factor affecting clam survival, explaining 45% of the total variability, whereas embayment, sites within embayments, tidal gradient, and intraspecific density collectively accounted for less than 10% of the variation. At all four intertidal sites, clam survival in experimental units designed to deter predators averaged 72%, but the degree of enhancement varied between embayments (PB = 61%; CB = 267%). Average survival rate was higher (by 12–16%), but growth was slower (by ca. 50%) in upper vs. lower intertidal blocks; however, the patterns differed for both variables between sites within each embayment. The effect of increasing intraspecific clam density was to lower survival by ca. 17% (56% [660 m^{-2}] vs. 48% [1320 m^{-2}]) in both embayments, but growth was unaffected. Overall, clams doubled in SL, although mean relative growth was 15% greater in CB than PB. Tidal gradient, sites within embayments, and blocks were the three most important factors explaining 35%, 19%, and 22% of total variation in relative clam growth, respectively. In Maine and the northeast US, juveniles of *Mya* reach their highest abundance above mean low tide levels. Experimental evidence presented here suggests that differential predation along the tidal gradient is the dominant factor controlling clam abundance and distribution patterns in the intertidal zone.
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1. Introduction

Over the past four decades, marine ecologists investigating the regulation of invertebrate populations within low-energy, shallow-water and intertidal soft-

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bottom communities have paid considerable attention to the role of predation and competition (Virnstein, 1977; Peterson, 1982a,b; Wilson, 1990; Thrush, 1999; Quijón and Snelgrove, 2005). Notwithstanding the current debate regarding the importance of pre- and post-settlement interactions in structuring these communities (Caley et al., 1996; Fraschetti et al., 2003), the present model for established residents of unvegetated soft sediments posits that predation (whether infaunal, epifaunal, partial, or complete) is more important in controlling the distribution and abundance of residents than competition for food or space (Micheli, 1997). This idea, first reviewed by Peterson (1979) and expanded by Commito and Ambrose (1985) and Ólafsson et al. (1994), has been supported generally by several experimental field investigations involving burrowing bivalves in the order Veneroida (Peterson, 1982b; Black and Peterson, 1988; Richards et al., 1999). The relative importance of predation is inferred from other studies where predator abundance primarily had a negative effect on prey abundance of taxa as diverse as polychaetes (Desroy et al., 1998; Beukema et al., 2000), amphipods (Hilton et al., 2002), and gastropods (Ray and Stoner, 1995). However, effects of predation and other biotic factors on population growth and recruitment may vary over different spatial scales (e.g., between sites outside different estuaries or within the same estuary, or along tidal gradients) complicating interpretations of how populations respond to these agents (Peterson and Beal, 1989; Micheli, 1996; Legendre et al., 1997; Constable, 1999; Seitz and Lipcius, 2001; Thrush et al., 2000).

Generalizations about population processes in marine soft-sediments largely have been developed based on a limited number of field sites and/or sampling times, and specific results from field experiments may vary depending on the spatial scale that trials are carried out (sensu Thrush et al., 2000). At least three experimental approaches have been adopted by benthic ecologists to examine how predation and other mechanisms vary over different spatial scales. One method is to manipulate the size of experimental units, prey patches, or habitats and examine how processes change across different levels of the factor (Whitlatch et al., 1997; Fernandes et al., 1999). Another is to conduct similar experiments at the same time in two or more ecosystems differing in scale (Seitz and Lipcius, 2001). A third approach, used here, is to establish the same experiment at two or more geographically distinct sites or different habitats to examine interactions between local- and broader-scale processes (Thrush et al., 2000).

Sedentary, intertidal marine bivalves afford a unique tool to test how spatial scales affect ecological processes because their densities are relatively easy to manipulate without large handling mortalities, predator exclusion is relatively straightforward, growth and survival rates of marked individuals are easily measured, and their effect on recruitment of con- and/or heterospecifics can be measured. The soft-shell clam, *Mya arenaria*, is a suspension-feeding bivalve that occurs subtidally and intertidally in the western Atlantic, from North Carolina to Newfoundland (Abbott, 1974). In the northeast U.S. and Canadian Maritimes, its greatest abundance, and nearly 100% of its commercial exploitation, occurs in the intertidal zone (Wallace, 1997). *Mya* is iteroparous, and its growth is size-, site-, and habitat-dependent (Brousseau, 1978, 1979). In Maine, USA, *Mya* grows seasonally from April to November when seawater temperatures are above 5 °C (Beal et al., 2001). Because annual growth rates are highest among juveniles (<12 mm shell length, SL), and these small individuals are more susceptible to epibenthic and infaunal predators than larger conspecifics, simultaneous field manipulations of 0-year class individuals across several locations should permit strong tests about the role of specific ecological processes.

The purpose of this manipulative field study was to examine over a 185-day growing season (May to November) the interactive effects of predation and intraspecific competition on growth and survival of juveniles of *Mya* over four spatial scales ranging from 0.05 km to 10's of km. The field experiment was conducted along a tidal gradient at each of two intertidal sites in lower Passamaquoddy Bay and upper Cobscook Bay in eastern Maine. Based on previous field trials with soft-shell clam juveniles (Beal, 1994; Beal et al., 2001), I expected that at every site survival would be affected most by predation. Further, I expected that predation intensity would be greatest in the lower intertidal zone because these areas are exposed to higher numbers of waterborne predators than in the upper intertidal zone. In addition, because intertidal bivalve growth typically is a function of time of tidal inundation (Peterson and Black, 1987), I anticipated that juvenile clams growing near the lower intertidal zone would be significantly larger than those growing near the upper intertidal zone at the end of the experiment. Density-dependent reduction in growth was anticipated only where resources were potentially in short supply (Weins, 1977); that is, at high shore levels where suspended food is temporally limited relative to lower on the shore.

2. Methods

2.1. Experimental animals

Juvenile soft-shell clams, *M. arenaria*, used in this study were hatchery-reared individuals obtained from the Beals Island Regional Shellfish Hatchery of the Downeast

Table 1
Latitude and longitude estimates for each of the two intertidal study sites within each of two embayments located in extreme eastern Maine

Site	Embayment	Tide level	Latitude	Longitude
Little River (LR)	Passamaquoddy Bay	Low	44° 58.34′ N	67° 04.03′ W
		High	44° 58.32′ N	67° 04.03′ W
Gleason Cove (GC)	Passamaquoddy Bay	Low	44° 58.12′ N	67° 03.33′ W
		High a	44° 58.09′ N	67° 03.52′ W
		High b	44° 58.04′ N	67° 03.45′ W
Half Moon Cove East (HW)	Cobscook Bay	Low	44° 57.13′ N	67° 03.08′ W
		High	44° 57.25′ N	67° 03.03′ W
Half Moon Cove West (HE)	Cobscook Bay	Low	44° 56.97′ N	67° 02.71′ W
		High	44° 57.20′ N	67° 02.56′ W

Due to the lack of sufficient space in the upper intertidal at Gleason Cove, blocks of experimental units were divided between two locations approximately 300 m apart.

Institute for Applied Marine Research and Education, Great Wass Island, Beals, Maine (44° 28.82′ N; 67° 35.92′ W). Animals (mean shell length [$\overline{X}_{SL}$]±95%

confidence interval=12.4±0.13 mm, n=100) were produced during the summer of 2002 and overwintered according to Beal et al. (1995).

2.2. Study sites

The study sites (Table 1; Fig. 1) were located in extreme east coastal Maine in the community of Sipayik, near Eastport, and were chosen to represent soft-sediment intertidal locations in southwestern Passamaquoddy Bay adjacent to Western Passage (PB: Little River flat and Gleason Cove, approximately 1.2 km apart, Euclidean distances) and northeastern Cobscook Bay (CB: Half Moon Cove East and Half Moon Cove West, approximately 1 km apart). The PB and CB sites are only 1.5–4 km apart by land, but approximately 18 km by water (Fig. 1). Although not specifically measured, upper intertidal sediments at each location were more compact, and contained more large particles (muddy sand, small gravel) compared to lower intertidal sediments that were unconsolidated with a higher percentage of silt and clay. Both embayments are macrotidal estuaries with a mean semidiurnal tidal range of 5.7 m (Brooks et al., 1999). Although each site contained commercial quantities of adults of the soft-shell clam, I am aware of commercial harvesting (sensu Robinson and Rowell, 1990) at only one site, Little River, which took place away from the experimental manipulation.

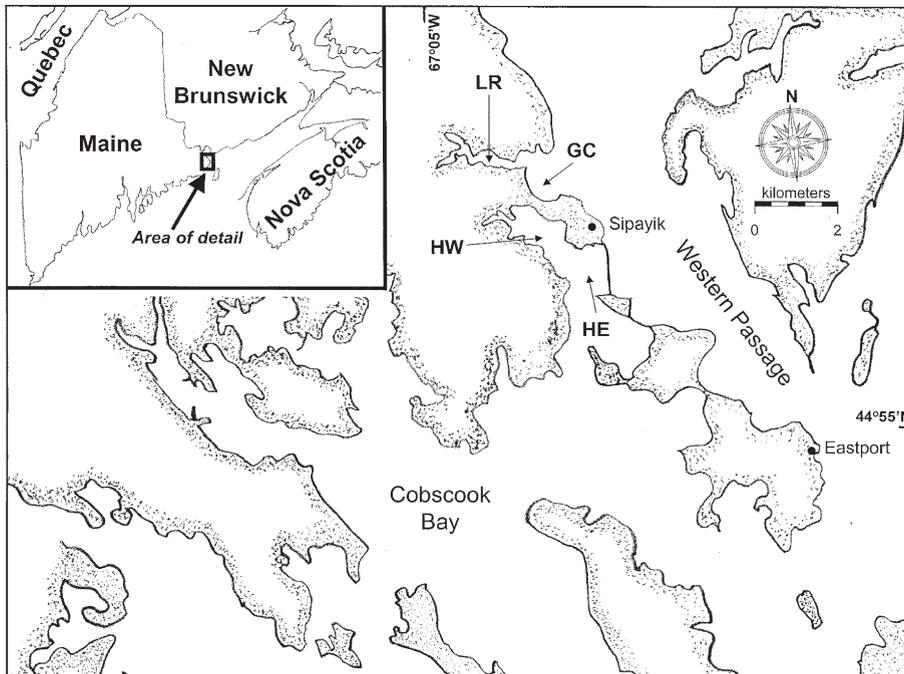
Fig. 1. Four intertidal study sites in eastern Maine, USA. See Table 1 for site abbreviations.

2.3. Experimental design

Identical field experiments were established at all four sites on 20 May 2003. Plastic horticultural pots (15.24 cm diameter × 15.24 cm deep, or 0.0182 m^2, as described in Beal et al. (2001), and henceforth referred to as experimental units) were filled completely with ambient sediments using garden trowels, and then forced into the excavated hole so that the rim was flush with the mud flat surface. Next, clams at one of two stocking densities ($12 \approx 660$ m^{-2}, or $24 \approx 1320$ m^{-2}) were pushed gently into the sediment within each experimental unit to a depth of 1 cm. The lowest density is within the range of densities of >1-yr old wild individuals reported by Commito (1982) from a nearby intertidal flat in eastern Maine (Federal Harbor, Lubec: 44° 51.33′ N; 67° 04.73′ W) from 1977–1979. Units were placed at an upper (exposed 2.5–3 h low tide^{-1}) and lower intertidal level (exposed < 0.5 h low tide^{-1}) at each study site. Half of the units at each tidal level were completely covered with a piece (30 cm × 30 cm) of plastic mesh netting (6.4 mm aperture; InterNet, Inc., Anoka, MN) to deter epibenthic predators. The netting was held in place using a rubber band that was affixed to the rim of each unit and each piece projected approximately 4 cm above the rim and mud flat surface. The remaining units allowed predator access, but kept clams within the experimental units with a narrow piece of mesh netting (10 cm wide × 35 cm long) that was secured around the circumference of each unit with a rubber band. When positioned in the sediments, the piece of netting (that acted as a flexible fence) protruded approximately 4 cm above the rim of each unit (this narrow piece of mesh netting does not deter predators or interfere with clam feeding and growth [Beal, 1994]). The experimental units with the mesh fencing henceforth are referred to as open enclosures (sensu Peterson and Beal, 1989).

To examine the importance of spatial heterogeneity within a tidal level, experimental units at each location were physically arrayed in five 2 × 4 blocks, with 1 m spacing between each row and column and 5 m spacing between adjacent blocks. Due to the lack of sufficient space within the upper intertidal zone at Gleason Cove, the five blocks were split between two locations approximately 300 m apart. Two replicates of each combination of stocking density ($a = 2$) and predator protection ($b = 2$) were used in each block making the design a generalized completely randomized block design (GCRBD; Underwood, 1997). A total of 320 experimental units (2 embayments × 2 locations within each embayment × 2 tidal heights × 2 levels of stocking density × 2 levels of netting × 5 blocks per location × 2 replicates per block) and 5760 clam juveniles were used in the study.

On 20 November 2003, after 185 days, all experimental units were removed from each site and the contents of each washed through a 1.4 mm sieve. All live clams were measured in two linear shell dimensions to the nearest 0.1 mm using Vernier calipers: initial and final SL. Although individual clams were not physically tagged or marked in May 2003, hatchery-reared individuals mark themselves uniquely when planted in the field forming a disturbance line that delineates their initial SL (Beal et al., 1999). All dead clams were categorized according to shell damage: 1) undamaged (death due to handling stress, disease, suffocation, or from predators such as *Cerebratulus lacteus*, the milky ribbon worm, that leave no shell damage [Beal and Vencile, 2001]); 2) crushed or chipped (typical of crab predation); or, 3) drilled (typical of naticid moon snail, *Euspira* spp., predation). In addition, since a known number of clams was added to each unit, number of missing individuals was recorded. The number of wild recruits (< 12 mm SL) was recorded for each experimental unit and, when present, measured as described above.

2.4. Statistics

Analysis of variance (ANOVA) was used to test hypotheses related to the experimental design. A decision rule of $\alpha = 0.05$ was used to determine statistical significance. Percent clam survival was arcsine-transformed to meet the variance homogeneity assumption of ANOVA. Counts of natural recruits per experimental unit were square root-transformed to meet ANOVA assumptions. Untransformed relative growth ([Final SL − Initial SL]/Initial SL) was used to estimate growth rather than an estimate for growth rate (Final SL − Initial SL)/185 days because there was a significant, linear relationship between final and initial SL ($r^2 = 0.148$, $P < 0.0001$, $n = 2912$). Means presented within the text, in tables, and figures are untransformed and are accompanied by their 95% confidence interval.

The following linear model from the experimental design was used to analyze the twenty-seven hypothesis tests (sources of variation) associated with mean survival, growth, and number of recruits:

$$
\begin{aligned}
Y_{ijklmno} = {} & \mu + A_i + B_j + AB_{ij} + C_k + AC_{ik} + BC_{jk} \\
& + ABC_{ijk} + D_l + AD_{il} + BD_{jl} + ABD_{ijl} + CD_{kl} \\
& + ACD_{ikl} + BCD_{jkl} + ABCD_{ijkl} + E(A)_{m(i)} \\
& + BE(A)_{jm(i)} + CE(A)_{km(i)} + DE(A)_{lm(i)} \\
& + BCE(A)_{jkm(i)} + BDE(A)_{jlm(i)} + CDE(A)_{klm(i)} \\
& + BCDE(A)_{jklm(i)} + F(ABE)_{n(ijm)} \\
& + CF(ABE)_{kn(ijm)} + DF(ABE)_{ln(ijm)} \\
& + CDF(ABE)_{kln(ijm)} + e_{o(ijklmn)}
\end{aligned}
$$

Table 2
Fate of hatchery-reared juveniles of the soft-shell clam, *Mya arenaria*, (initial mean shell length [SL]$=12.4\pm0.13$ mm) at four locations in eastern Maine over a 185-d period from 20 May to 20 November 2003

Tidal height	Density # m^{-2}	Protection	*A*	DU	DC	DD	M
Location: Passamaquoddy Bay: Little River							
High	660	−	52.5 (12.6)	5.0 (4.2)	0.0 (0.0)	0.0 (0.0)	42.5 (13.3)
	660	+	75.8 (17.7)	12.5 (16.4)	0.8 (1.9)	0.0 (0.0)	10.9 (9.8)
	1320	−	41.3 (19.1)	8.3 (0.9)	0.8 (1.3)	0.0 (0.0)	49.6 (17.8)
	1320	+	63.8 (15.0)	19.6 (11.7)	0.4 (0.9)	0.0 (0.0)	16.2 (8.4)
Low	660	−	60.8 (11.6)	2.5 (2.8)	1.7 (0.0)	0.0 (0.0)	35.0 (14.3)
	660	+	74.2 (13.4)	8.3 (3.9)	3.3 (2.9)	0.0 (0.0)	14.2 (11.6)
	1320	−	49.2 (27.7)	2.9 (2.8)	5.8 (3.2)	0.0 (0.0)	42.1 (16.1)
	1320	+	61.3 (9.2)	8.8 (5.2)	2.9 (2.0)	0.0 (0.0)	27.1 (9.6)
Location: Passamaquoddy Bay: Gleason Cove							
High	660	−	45.8 (12.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	54.2 (13.0)
	660	+	85.0 (9.7)	0.8 (1.9)	0.0 (0.0)	0.0 (0.0)	14.2 (8.9)
	1320	−	38.8 (17.7)	0.4 (0.9)	0.4 (0.9)	0.0 (0.0)	60.4 (17.3)
	1320	+	81.3 (6.0)	1.3 (2.0)	0.8 (1.3)	0.0 (0.0)	16.6 (4.3)
Low	660	−	43.3 (10.0)	0.8 (1.9)	0.0 (0.0)	0.0 (0.0)	55.8 (10.1)
	660	+	62.5 (7.0)	3.3 (4.2)	2.5 (2.9)	0.0 (0.0)	31.7 (6.8)
	1320	−	19.2 (12.7)	0.4 (0.9)	0.8 (1.3)	0.0 (0.0)	79.6 (12.9)
	1320	+	61.3 (11.9)	4.2 (3.7)	1.3 (2.0)	0.0 (0.0)	33.3 (12.1)
Location: Cobscook Bay: Half Moon Cove (West)							
High	660	−	31.7 (19.6)	1.7 (2.5)	0.8 (1.9)	0.0 (0.0)	65.8 (19.4)
	660	+	76.7 (19.8)	2.5 (2.9)	0.8 (1.9)	0.0 (0.0)	20.0 (17.6)
	1320	−	35.8 (15.6)	2.1 (2.5)	0.4 (0.9)	0.0 (0.0)	61.7 (14.3)
	1320	+	65.0 (12.9)	4.2 (3.8)	2.1 (2.9)	0.0 (0.0)	28.7 (12.5)
Low	660	−	24.2 (11.1)	1.7 (2.5)	2.5 (2.9)	0.0 (0.0)	71.6 (11.7)
	660	+	72.5 (6.3)	9.2 (4.4)	1.7 (2.5)	0.0 (0.0)	16.6 (6.3)
	1320	−	12.9 (12.0)	2.5 (3.2)	1.3 (1.9)	2.1 (4.7)	81.2 (14.9)
	1320	+	69.6 (9.1)	7.9 (2.9)	2.1 (2.1)	0.0 (0.0)	20.4 (6.3)
Location: Cobscook Bay: Half Moon Cove (East)							
High	660	−	16.7 (10.5)	3.3 (5.8)	2.5 (4.0)	2.5 (2.9)	75.0 (12.9)
	660	+	80.0 (6.4)	4.2 (5.1)	0.8 (1.9)	0.0 (0.0)	15.0 (6.2)
	1320	−	15.0 (7.2)	0.8 (1.3)	2.1 (2.9)	0.0 (0.0)	82.1 (14.3)
	1320	+	80.4 (5.6)	4.6 (3.3)	0.8 (1.3)	0.0 (0.0)	14.2 (4.0)
Low	660	−	15.0 (10.1)	0.0 (0.0)	0.8 (1.9)	18.3 (21.2)	65.9 (18.7)
	660	+	78.3 (8.9)	5.0 (4.2)	1.7 (2.5)	0.0 (0.0)	15.0 (8.8)
	1320	−	8.8 (4.8)	0.8 (1.3)	0.4 (0.9)	10.0 (10.2)	80.4 (8.9)
	1320	+	64.2 (7.0)	5.4 (4.5)	1.7 (2.1)	0.0 (0.0)	28.7 (6.8)

Five blocks with each of eight experimental units (plastic horticultural pots$=0.0182$ m^2) were arrayed in a 2×4 matrix (1 m spacing between rows and columns and 5 m spacing between adjacent blocks) at each tidal height at each site. Two replicates of each of four treatments were randomly assigned to units within each block (Treatments$=12$ clams [660 m^{-2}], netting present; 12 clams, netting absent; 24 clams [1320 clams m^{-2}], netting present; 24 clams, netting absent). "Netting" refers to black, plastic, flexible netting with a 6.4 mm aperture. ($A=\%$ *A*live; DU$=\%$ *D*ead, with *U*ndamaged valves, DC$=\%$ *D*ead, with *C*rushed or *C*hipped valves, DD$=\%$ *D*ead, with a countersunk *D*rill hole (due to moon snail predators), and M$=\%$ *M*issing. Means$\pm95\%$ confidence intervals are given pooled across blocks ($n=10$).

Where:

μ = Theoretical mean;

A_i = Embayment ($a=2$ levels: Passamaquoddy Bay (PB) vs. Cobscook Bay (CB); factor is fixed);

B_j = Tidal height ($b=2$ levels: high intertidal vs. low intertidal; factor is fixed);

C_k = Density ($c=2$ levels: 660 vs. 1320 individuals m^{-2}; factor is fixed);

D_l = Protection ($d=2$ levels: open enclosures vs. units covered with netting; factor is fixed);

E_m = Site(Embayment) ($e=2$ levels within each embayment [Passamaquoddy Bay: Little River (LR) vs. Gleason Cove (GC); Cobscook Bay: Half Moon Cove west (HW) vs. Half Moon Cove west (HE)]; factor is fixed;

F_n = Block ($d=5$ levels: 1, 2, 3, 4, 5; factor is random); and

$e_{o(ijklmn)}$ = Experimental error associated with the $n=2$ replicates per combination of treatments.

I used Underwood (1997) to determine appropriate mean square estimates for each source of variation. In addition, I decomposed several sources of variation into meaningful contrasts and followed the advice of Winer et al. (1991) by using an adjusted alpha ($\alpha' = 1 - [1-\alpha]^{1/n}$; where $\alpha = 0.05$ and $n =$ number of contrasts) as a decision rule to avoid excessive type I errors.

3. Results

3.1. Survival

Mean survival pooled across all factors was $51.9 \pm 3.16\%$ ($n = 320$), and ranged from a low of $8.8 \pm 4.8\%$ ($n = 10$) in open enclosures stocked at 1320 m^{-2} in low intertidal blocks at HE in CB to a high of $85 \pm 9.7\%$ ($n = 10$) in protected units stocked at 660 m^{-2} in high intertidal blocks at GC in PB (Table 2).

3.1.1. Embayments and sites

Clam survival varied significantly ($P < 0.0001$) between embayments (Tables 2 and 3). Overall mean survival was approximately 22% higher in PB than in CB ($\overline{X}_{PB} = 57.2 \pm 3.8\%$ vs. $\overline{X}_{CB} = 46.7 \pm 4.9\%$; $P < 0.0001$, $n = 160$), and is likely due to the difference in mean number of clams missing from open enclosures between the two embayments (Table 2). Mean missing rate of clams in open enclosures at the two CB sites was $72.9 \pm 4.5\%$ com-

Table 3

Analysis of variance results on the arcsine-transformed mean percent alive data for juvenile soft-shell clams, *Mya arenaria*, at four intertidal locations in eastern Maine over a 185-day period between 20 May and 20 November 2003

Source of variation	df	SS	% Variation	MS	F	Pr > F
Bay	1	5498.66	4.04	5498.66	42.33	**<0.0001**
Tide	1	2253.49	1.65	2253.49	17.35	**0.0002**
Bay*Tide	1	0.58	<1.00	0.58	0.00	0.9470
Density	1	2753.66	2.02	2753.66	16.29	**0.0003**
Bay*Density	1	495.90	<1.00	495.90	2.93	0.0964
Tide*Density	1	329.94	<1.00	329.94	1.95	0.1720
Bay*Tide*Density	1	57.80	<1.00	57.80	0.34	0.5628
Protect	1	61204.23	45.08	61204.23	263.09	**<0.0001**
Bay*Protect	1	6727.65	4.95	6727.65	28.92	**<0.0001**
Tide*Protect	1	71.45	<1.00	71.45	0.31	0.5833
Bay*Tide*Protect	1	540.63	<1.00	540.63	2.32	0.1372
Density*Protect	1	8.45	<1.00	8.45	0.03	0.8699
Bay*Density*Protect	1	204.89	<1.00	204.89	0.66	0.4224
Tide*Density*Protect	1	516.53	<1.00	516.53	1.66	0.2062
Bay*Tide*Density*Protect	1	1.25	<1.00	1.25	0.00	0.9497
Site(Bay)	2	898.56	<1.00	449.28	3.46	**0.0437**
Passamaquoddy Bay: LR vs. GC	1	580.83	<1.00	580.83	4.47	0.0424
Cobscook Bay: HW vs. HE	1	317.73	<1.00	317.73	2.45	0.1274
Tide*Site(Bay)	2	2050.03	1.51	1025.01	7.89	**0.0016**
Passamaquoddy Bay	1	2032.09	1.49	2032.09	15.64	**0.0004**
Cobscook Bay	1	17.94	<1.00	17.94	0.14	0.7126
Density*Site(Bay)	2	33.59	<1.00	16.79	0.10	0.9057
Protect*Site(Bay)	2	2487.76	1.83	1243.88	5.35	**0.0099**
Passamaquoddy Bay	1	1360.81	1.00	1360.81	5.85	**0.0214**
Cobscook Bay	1	1126.95	<1.00	1126.95	4.84	0.0351
Tide*Density*Site(Bay)	2	71.91	<1.00	35.95	0.21	0.8095
Tide*Protect*Site(Bay)	2	304.35	<1.00	152.17	0.65	0.5267
Density*Protect*Site(Bay)	2	368.30	<1.00	184.15	0.59	0.5584
Tide*Density*Protect*Site(Bay)	2	900.12	<1.00	450.06	1.45	0.2495
Block(Bay*Site*Tide)	32	4156.99	3.06	129.90	0.99	0.4946
Protect*Block(Bay*Site*Tide)	32	7444.43	5.48	232.63	1.77	**0.0118**
Density*Block(Bay*Site*Tide)	32	5408.37	3.98	169.01	1.28	0.1595
Density*Protect*Block(Bay*Site*Tide)	32	9929.49	7.31	310.29	2.36	**0.0003**
Error	160	21057.89	15.51	131.61		
Total	319	135777.10				

Boldface P-values are statistically significant. Several sources of variation were decomposed into their orthogonal components and, to control for excessive type I errors, $\alpha' = 0.0253$ was used as the decision rule. % Variation indicates percent of total variation explained by each source of variation. See Table 1 for site abbreviations. ($n = 2$).
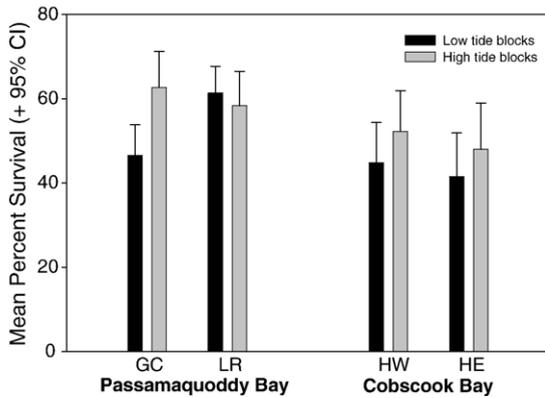
Fig. 2. Mean percent survival of juvenile soft-shell clams (initial mean SL=12.4±0.13 mm) planted at each of two sites and tidal heights within two embayments in eastern Maine from 20 May to 20 November 2003. See Table 1 for site and embayment information. Means are pooled over density and protection treatments, as well as blocks, within each site. (n=40).

pared to 52.4±5.2% at the PB sites (n=80). The source of variation due to sites nested with embayment was statistically significant (P=0.0437; Table 3), but when decomposed into its two single degree-of-freedom orthogonal components, neither one was significant. For example, there was a 9.5% difference in mean survival between the two PB sites ($\overline{X}_{GC}$=54.6±5.8% vs. $\overline{X}_{LR}$=59.8±5.1%, n=80) and an 8.3% difference between the two CB sites ($\overline{X}_{HW}$=48.5±6.7% vs. $\overline{X}_{HE}$=44.8±7.4%, n=80). Together, embayments and sites explained approximately 5% of the total variation associated with mean percent survival (Table 3).

3.1.2. Tidal height

Clams planted in units near the high intertidal had significantly higher survival rates (55.3±4.6%, n=160) than those near the low intertidal (48.6±4.3%; P=0.0002, n=160; Table 3), but tidal height effects also varied significantly between sites within each embayment (P=0.0016, Table 3; Fig. 2). In CB, mean survival at both sites was 16–17% greater in high vs. low blocks. In PB at GC, the trend was similar, although the difference was larger (ca. 35%). At LR, where the physical distance between high and low tide blocks was the smallest of any of the four sites (ca. 40 meters; Table 1; Fig. 1), no significant differences were observed in mean survival between high (58.3±8.1%, n=40) and low tide blocks (61.4±6.3%, n=40).

3.1.3. Intraspecific density

Clams added to experimental units at 660 m^{-2} had approximately 17% higher survival rates than those

planted at 1320 m^{-2} (55.9±4.4% vs. 47.9±4.5%, respectively; P=0.0003, n=160; Table 3).

3.1.4. Predator exclusion

Predator deterrent netting significantly enhanced clam survival, but the mean difference between open enclosures and protected units varied between embayments (P<0.0001) and sites within embayments (P=0.0099; Table 3). Survival within protected units was not significantly different between embayments ($\overline{X}_{PB}$=70.6±4.0% vs. $\overline{X}_{CB}$=73.3±3.4%; P=0.6570, n=80), however, there was nearly a 120% difference in mean survival within open units between embayments ($\overline{X}_{PB}$=43.9±5.0% vs. $\overline{X}_{CB}$=20.0±4.1%; P<0.0001, n=80). Netting enhanced survival from 2.7 to 5.5 times at the CB sites but only by 1.3 to 1.9 times at the PB sites (Fig. 3). Approximately 45% of the total variation in mean percent survival was explained by the main effect due to predator exclusion (Table 3), which was an order of magnitude higher than any other main factor in this study.

3.1.5. Spatial variation due to blocks

Two of four sources of variation associated with the field blocks were significant (P<0.02; Table 3), and, collectively, these sources explained nearly 20% of the total variation implying the importance of spatial variability on survival at scales ca. 5 m. Decomposing the 32 df associated with the Protect*Block(Bay*Site*Tide) source of variation into eight 4 df sums of squares and using an α'=0.0064 (Winer et al., 1991) as the decision rule, revealed that mean survival between open enclosures and protected units varied significantly (P=0.0042) from block-to-block at only one embayment, site, and tidal
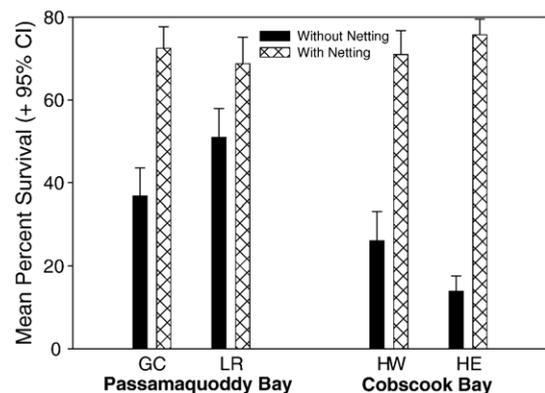

Fig. 3. Interaction plot demonstrating how mean survival varies between open enclosures and protected experimental units across two sites within each of two embayments in eastern Maine. Plot depicts the source of variation listed in Table 3 as Protect*Site (Bay), P=0.0099. See Table 1 for site and embayment information. (n=40).

Table 4

Analysis of variance results on the untransformed mean relative growth data for juvenile soft-shell clams, *Mya arenaria*, at four intertidal areas in eastern Maine (two sites in Passamaquoddy Bay and two in Cobscook Bay) from 20 May to 20 November 2003

Source of variation	df	SS	% Variation	MS	F	Pr>F
Bay	1	2.000	3.96	2.000	19.07	**0.0001**
Tide	1	17.528	34.73	17.528	167.12	**<0.0001**
Bay*Tide	1	2.617	5.18	2.617	24.95	**<0.0001**
Density	1	0.001	<1.00	0.001	0.01	0.9078
Bay*Density	1	0.064	<1.00	0.064	0.67	0.4181
Tide*Density	1	0.006	<1.00	0.006	0.07	0.7971
Bay*Tide*Density	1	0.025	<1.00	0.025	0.27	0.6100
Protect	1	0.219	<1.00	0.219	4.03	0.0533
Bay*Protect	1	0.166	<1.00	0.166	3.05	0.0902
Tide*Protect	1	0.000	<1.00	0.000	0.00	0.9490
Bay*Tide*Protect	1	0.078	<1.00	0.078	1.44	0.2386
Density*Protect	1	0.018	<1.00	0.018	0.20	0.6587
Bay*Density*Protect	1	0.027	<1.00	0.027	0.30	0.5907
Tide*Density*Protect	1	0.015	<1.00	0.015	0.17	0.6849
Bay*Tide*Density*Protect	1	0.017	<1.00	0.017	0.19	0.6670
Site(Bay)	2	9.658	19.14	4.829	46.04	**<0.0001**
Passamaquoddy Bay: LR vs. GC	1	3.479	6.89	3.479	33.17	**<0.0001**
Cobscook Bay: HW vs. HE	1	6.179	12.25	6.179	58.91	**<0.0001**
Tide*Site(Bay)	2	0.105	<1.00	0.052	0.50	0.6088
Density*Site(Bay)	2	0.093	<1.00	0.046	0.49	0.6184
Protect*Site(Bay)	2	0.091	<1.00	0.045	0.84	0.4419
Tide*Density*Site(Bay)	2	0.018	<1.00	0.009	0.10	0.9086
Tide*Protect*Site(Bay)	2	0.032	<1.00	0.016	0.30	0.7450
Density*Protect*Site(Bay)	2	0.035	<1.00	0.017	0.19	0.8285
Tide*Density*Protect*Site(Bay)	2	0.019	<1.00	0.009	0.10	0.9042
Block(Bay*Site*Tide)	32	3.356	6.65	0.104	2.12	**0.0014**
Protect*Block(Bay*Site*Tide)	32	1.747	3.46	0.054	1.10	0.3387
Density*Block(Bay*Site*Tide)	32	3.049	6.04	0.095	1.92	**0.0049**
Density*Protect*Block(Bay*Site*Tide)	29	2.741	5.43	0.094	1.91	**0.0069**
Error	146	7.229	14.32	0.049		
Total	302	50.469				

Boldface *P*-values are statistically significant. The source of variation listed as Site (Bay) was decomposed into two single degree-of-freedom contrasts and a decision rule of $\alpha' = 0.0253$ was used to determine statistical significance. % Variation indicates the percent of total variation explained by each source of variation. $n = 1$ or 2 depending on survival rate.

Table 5

Mean final SL±95% CI (in mm), and minimum and maximum final SL for soft-shell clams, *Mya arenaria*, at two sites within each of two embayments in eastern Maine from 20 May to 20 November 2003

Embayment	Site	Tide height	n	Mean SL (±95% CI)	Minimum SL	Maximum SL
Passamaquoddy	LR	High	40	23.0 (0.54)	19.9	26.9
		Low	40	28.2 (0.77)	21.8	32.2
		Pooled	80	25.6 (0.74)		
	GC	High	40	27.3 (0.89)	20.7	31.8
		Low	37	29.8 (0.69)	26.7	35.1
		Pooled	77	28.5 (0.63)		
Cobscook	HW	High	37	21.8 (0.65)	14.1	25.6
		Low	36	30.3 (0.85)	21.9	37.6
		Pooled	73	26.0 (1.13)		
	HE	High	37	27.1 (0.73)	23.2	31.2
		Low	36	34.3 (0.83)	26.9	39.5
		Pooled	73	30.6 (0.99)		

Mean SL of clams at the beginning of the field experiment was 12.4±0.13 mm. *n* refers to the number of experimental units with one or more living clams. See Table 1 for description of each site.
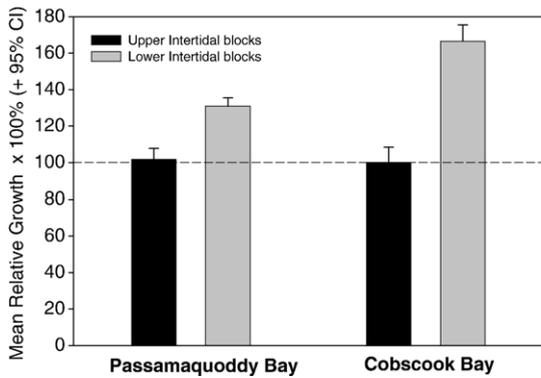
Fig. 4. Growth of juveniles of *Mya arenaria* from 20 May to 20 November 2003 in upper and lower intertidal blocks within each of two embayments in eastern Maine. Mean relative growth is presented as a percentage. 100% (dotted line) indicates a doubling of shell length. Clams grew significantly faster in experimental units in low intertidal blocks in both embayments, but differences between tidal heights were more pronounced in Cobscook vs. Passamaquoddy Bay ($P<0.0001$; Table 4). (n varies between 36 and 40).

height: CB, HW, high intertidal. The presence of netting led to a significant enhancement in mean survival, except in one block at that location. In addition, the significant source of variation associated with Density*Protect*Block (Bay*Site*Tide) ($P=0.0003$; Table 3) was due to a significant Density*Protection interaction across blocks only at the high intertidal at HW ($P<0.0001$). In open enclosures, a low density refuge was observed in two blocks and a high density refuge was observed in two blocks while no difference was observed in the other block.

3.2. Growth

On average, clams added 15.1 ± 0.49 mm ($n=303$) of new shell from May to November 2003, which was equivalent to a mean relative growth (rg) ($\times100\%$) of $124.1\pm4.62\%$. Slowest growth was observed in CB at HW in protected units stocked at 660 m^{-2} ($67.7\pm24.49\%$; $\overline{X}_{SL}=21.5\pm1.99$ mm, $n=10$). Fastest growth was observed in CB at HE in open enclosures stocked at 1320 m^{-2} ($199.1\pm23.1\%$; $\overline{X}_{SL}=33.6\pm2.47$ mm, $n=9$).

3.2.1. Embayments and sites

Clams more than doubled their initial SL in each embayment; however, relative growth varied significantly between embayments. Mean rg was approximately 15% greater in CB than in PB (rg$\times100\%=116.1\pm4.4\%$, $n=157$ vs. $132.8\pm8.2\%$, $n=146$; $P<0.0001$, Table 4). The actual mean difference in SL between the two embayments was 1.3 mm ($\overline{X}_{CB}=28.3\pm0.83$ mm vs. $\overline{X}_{PB}=27.0\pm0.53$ mm). Sites nested within embayments

accounted for nearly 20% of the total variation in rg, with the highest proportion of variability explained by differences between the two locations in CB (Table 4). For example, mean SL was approximately 18% greater at HE than HW (30.6 ± 0.99 mm vs. 26.0 ± 1.13 mm, $n=73$; Table 5).

3.2.2. Tidal height

Differences in mean rg along the tidal gradient explained nearly 35% of the total variation of this dependent variable. Mean rg and mean SL were nearly 50% greater in low vs. upper intertidal blocks ($\overline{X}_{SL\ low}=30.6\pm0.52$ mm, $n=149$ vs. $\overline{X}_{SL\ high}=24.8\pm0.52$ mm, $n=154$); however, the mean difference between tidal heights was more pronounced in CB vs. PB (Fig. 4). In addition, mean rg (pooled over density and tidal height)
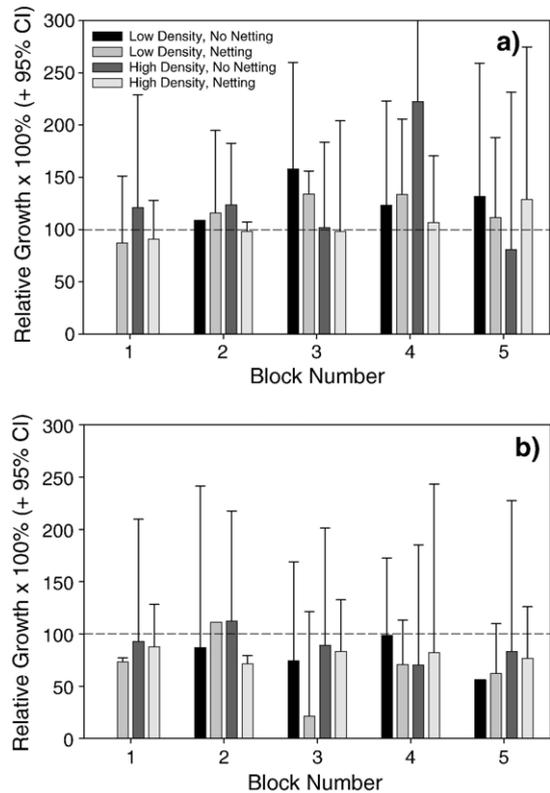

Fig. 5. Growth of soft-shell clam juveniles in upper intertidal blocks from 20 May to 20 November 2003 in a) Half Moon Cove East ($P<0.0001$) and b) Half Moon Cove West ($P>0.05$). Interaction plot demonstrates two of eight components of the source of variation listed as Density*Protect*Block(Bay*Site*Tide) in Table 4. Half Moon Cove East was the only one of the eight components that was statistically significant. Half Moon Cove West is included for comparison only, but shows overall difference in mean relative growth between these two sites that are located in Cobscook Bay. The dotted line at 100% represents a doubling of shell length. ($n=2$).

Table 6

Analysis of variance results on the square root-transformed mean number of wild clam, *Mya arenaria*, juveniles in experimental units on 20 November 2003, 185 days after field trials were initiated at two embayments and two intertidal sites within each embayment in eastern Maine

Source of variation	df	SS	% Variation	MS	F	Pr>F
Bay	1	4.851	1.52	4.851	4.73	**0.0372**
Tide	1	49.491	15.52	49.491	48.24	**<0.0001**
Bay*Tide	1	8.497	2.66	8.497	8.28	**0.0071**
Density	1	0.032	<1.00	0.032	0.10	0.7550
Bay*Density	1	0.001	<1.00	0.001	0.00	0.9480
Tide*Density	1	0.000	<1.00	0.000	0.00	0.9802
Bay*Tide*Density	1	0.000	<1.00	0.000	0.00	0.9715
Protect	1	34.837	10.92	34.837	51.90	**<0.0001**
Bay*Protect	1	0.006	<1.00	0.006	0.01	0.9243
Tide*Protect	1	5.389	1.69	5.389	8.03	**0.0079**
Bay*Tide*Protect	1	0.419	<1.00	0.419	0.63	0.4350
Density*Protect	1	0.006	<1.00	0.006	0.01	0.9338
Bay*Density*Protect	1	0.234	<1.00	0.234	0.27	0.6060
Tide*Density*Protect	1	0.268	<1.00	0.268	0.31	0.5811
Bay*Tide*Density*Protect	1	0.546	<1.00	0.546	0.63	0.4321
Site(Bay)	2	21.720	6.81	10.860	10.59	**0.0003**
Passamaquoddy Bay: LR vs. GC	1	5.348	1.68	5.348	5.21	0.0292
Cobscook Bay: HW vs. HE	1	16.372	5.13	16.372	15.96	**<0.0001**
Tide*Site(Bay)	2	5.917	1.85	2.958	2.88	0.0705
Density*Site(Bay)	2	0.088	<1.00	0.044	0.13	0.8753
Protect*Site(Bay)	2	17.137	5.37	8.568	12.76	**<0.0001**
Passamaquoddy Bay	1	14.128	4.43	14.128	21.06	**<0.0001**
Cobscook Bay	1	3.009	<1.00	3.009	4.48	0.0421
Tide*Density*Site(Bay)	2	0.117	<1.00	0.058	0.18	0.8374
Tide*Protect*Site(Bay)	2	3.412	1.07	1.706	2.54	0.0945
Density*Protect*Site(Bay)	2	1.235	<1.00	0.617	0.72	0.4966
Tide*Density*Protect*Site(Bay)	2	0.785	<1.00	0.392	0.45	0.6386
Block(Bay*Site*Tide)	32	32.828	10.29	1.025	2.30	**0.0004**
Protect*Block(Bay*Site*Tide)	32	21.481	6.73	0.671	1.50	0.0539
Density*Block(Bay*Site*Tide)	32	10.539	3.30	0.329	0.74	0.8441
Density*Protect*Block(Bay*Site*Tide)	32	27.624	8.67	0.863	1.93	**0.0043**
Error	160	71.498	22.42	0.446		
Total	319	318.969				

Boldface *P*-values are statistically significant. The source of variation listed as Site (Bay) was decomposed into two single degree-of-freedom contrasts and a decision rule using an $\alpha' = 0.0253$ used to determine statistical significance. % Variation indicates the percent of total variation explained by each source of variation. ($n = 2$).

differed significantly between the two sites within each embayment (Table 4). In both embayments, rg and final SL of clams at the easternmost location were greater than those at the westernmost location. For example, in PB, rg was 29.2% greater at GC than LR and, in CB, rg was 36.4% greater at HE than HW. Mean difference in final SL between the two PB and CB sites was nearly 3 mm and 5 mm, respectively (Table 5).

3.2.3. Intraspecific density

There was no significant effect of increasing intraspecific density on clam growth ($P = 0.9078$, Table 4). Mean rg was $124.9 \pm 6.7\%$ ($\overline{X}_{SL} = 28.3 \pm 0.71$ mm, $n = 150$) at the lower density ($660\ m^{-2}$) compared to $123.4 \pm 6.5\%$ ($\overline{X}_{SL} = 27.0 \pm 0.67$ mm, $n = 153$) at the higher density ($1320\ m^{-2}$).

3.2.4. Predator exclusion

Excluding predators using flexible netting had no significant effect on clam growth ($P = 0.0533$, Table 4). Mean rg was $126.2 \pm 7.04\%$ ($\overline{X}_{SL} = 27.8 \pm 0.69$ mm, $n = 143$) in open enclosures vs. $122.3 \pm 6.13\%$ ($\overline{X}_{SL} = 27.5 \pm 0.70$ mm, $n = 160$) for clams in units protected by deterrent netting.

3.2.5. Spatial variation due to blocks

The four sources of variation due to blocks explained nearly 15% of total variation in mean rg. Growth rates varied between blocks at two upper intertidal locations ($P = 0.0014$; Table 4). At GC, where two groups of upper intertidal blocks were approximately 300 m apart, clams grew 13% faster in one group of blocks than in the other. At the upper intertidal of HE, mean clam growth varied approximately 25% from block-to-block. In addition, the

effect of stocking density varied across the same blocks at HE ($P=0.0049$; Table 4). For example, clams from high density units grew approximately 18% faster than those from low density units in two blocks whereas no significant difference in growth between densities was observed in the other three blocks. Similarly, the significant source of variation listed as Density*Protect*Block (Bay*Site*Tide) in Table 4 ($P=0.0069$) was due to a Density × Protection interaction between blocks at the upper intertidal at HE (Fig. 5).

3.3. Wild recruits

A total of 524 wild clam recruits was recovered from the 320 experimental units in November 2003 (89.9 ± 20.24 m^{-2}; $\overline{X}_{SL}=4.2\pm0.3$ mm, size range$=1.4$–8.2 mm). Highest average abundance (456.0 ± 150.9 m^{-2}, $n=10$) occurred in high intertidal blocks in CB at HW in protected units stocked at 660 m^{-2}. Only one instance of zero recruits was observed (HE in CB in open enclosures stocked at 1320 m^{-2} in low intertidal blocks).

3.3.1. Embayments and sites

Mean number of *Mya* recruits varied significantly between embayments ($P=0.0372$), Table 6. Approximately 46% more wild juveniles were recovered from experimental units in CB ($\overline{X}=1.9\pm0.54$) individuals unit^{-1} $n=160$) compared with PB ($\overline{X}=1.3\pm0.49$ individuals^{-1} $n=160$). Significant differences were observed between sites in CB, where mean number per units was 3.4 times higher at HW than HE, but not in PB (Table 6, Fig. 6). Embayments and sites together explained only 8.3% of the total variation in number of recruits.
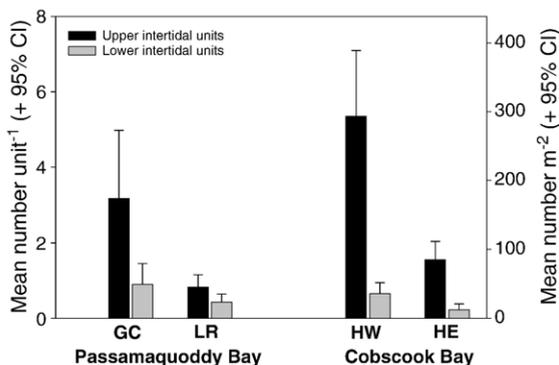

Fig. 6. Mean number of wild soft-shell clam recruits in upper and lower intertidal experimental units (and m^{-2}) at both sites within each embayment (see Table 1 for embayment and site descriptions). ANOVA (Table 6) indicated significant Bay × Tidal Height ($P=0.0071$) and Site (Bay) ($P=0.0003$) sources of variation. ($n=2$).

3.3.2. Tidal height

In general, more recruits were found in upper vs. lower intertidal units within both embayments, however, the differences between tidal heights was more pronounced in CB (8×) than in PB (3×) (Fig. 6). By itself, tidal height explained approximately 16% of the total variation in number of recruits per unit, second only to the percent explained by the smallest spatial scale measured — from unit to unit within the blocks (22.4%, Table 6).

3.3.3. Intraspecific density

Initial clam density had no effect on mean number of recruits per unit ($P=0.7550$, Table 6). Mean number was 90.3 ± 32.38 m^{-2} and 89.6 ± 24.66 m^{-2} in units stocked at 660 and 1320 m^{-2}, respectively.

3.3.4. Predator exclusion

Deterring predators led to an overall 3-fold enhancement of numbers of recruits, but this effect varied between tidal heights ($P=0.0079$) and sites ($P<0.0001$; Table 6). In upper intertidal blocks, approximately 3.2 times more wild juvenile clams were present in units protected with netting vs. open enclosures whereas the enhancement was nearly 3.6 times in lower intertidal blocks. The presence of protective netting was associated with an enhancement of recruits in three of four sites; however, this was not the case at LR in PB where mean number in open enclosures (0.6 ± 0.26 individuals, $n=40$) vs. protected units (0.7 ± 0.31 individuals, $n=80$) was not significantly different ($P=0.5953$). Predator exclusion explained approximately 11% of the total variation in mean number of recruits per experimental unit (Table 6).

3.3.5. Spatial variation due to blocks

Sources of variation involving blocks and interactions due to blocks explained the highest proportion of total variation of number of recruits (28.9%; Table 6). Mean number of recruits varied between blocks at the upper intertidal at one site in both embayments (source of variation listed as Block(Bay*Site*Tide) in Table 6). At GC in PB there was an approximate 8-fold difference in mean number of recruits between blocks ($P=0.0007$; minimum vs. maximum mean$=0.9\pm1.22$ and 7.5 ± 8.55 individuals unit^{-1} [49.5 vs. 414.8 m^{-2}], $n=8$). At HW in CB there was nearly a 3-fold difference ($P=0.0034$; minimum vs. maximum mean$=3.5\pm2.14$ and 10.1 ± 7.07 individuals unit^{-1} [192.3 vs. 554.9 m^{-2}], $n=8$). In addition, only one site and tidal height (upper intertidal at HW) contributed to the highly significant source of variation ($P=0.0043$) listed as Density*Protect*Block(Bay*Site*Tide) in

Table 6. For example, in one block, more recruits occurred in experimental units protected with netting at both densities while in another block no enhancement occurred at either density. In the other three blocks, more recruits occurred in protected units at one density, but not the other.

4. Discussion

Manipulative field experiments are important tools ecologists can use to understand the relative importance of factors affecting the dynamics of marine populations (but see Raffaelli and Moller, 1999). Experiments conducted at a single location or time, however, are unable to predict how mechanisms that control populations might vary in different physical settings or other times. By conducting the same experiment at several locations at the same time, an approach that has improved our understanding of the ecology of hard bottoms (e.g., Menge et al., 1994; Osman and Whitlatch, 2004) and soft-bottoms (Thrush et al., 2000; Seitz and Lipcius, 2001), one can assess whether the relative importance of local ecological processes vary at broader spatial scales. For example, Beal et al. (2001) concluded that predation, rather than competition, was more important in regulating populations of soft-shell clam juveniles at one intertidal flat in eastern Maine from April to December 1996. Similar conclusions were reached by Beal and Kraus (2002) who examined survival of _Mya_ juveniles at two tidal flats within 20 km of each other in eastern Maine during 1990 and 1991. Neither of these studies, however, attempted to determine the relative importance of these ecological processes at spatial scales larger than a single field site. This study was designed to assess how mechanisms controlling established populations of soft-shell clam juveniles vary spatially across four orders of magnitude from embayments 10,000's of meters apart to blocks nested within embayments, sites, and tidal levels that were several meters apart.

4.1. Spatial scales

Each of the three dependent variables measured in this study (survival, growth, and abundance of recruits) varied significantly across the largest spatial scales-embayments and sites; however, the relative importance of spatial scale differed between variables. For example, embayment and site together explained approximately 5%, 23%, and 8% of the total variation in clam survival, growth, and recruitment, respectively. Clam survival was 22% lower, growth faster by 15%, and recruitment of wild clams 46% greater in CB than in PB. Without netting to deter predators, nearly 75% of clams (independent of density and

tidal height) were missing from experimental units at the two CB sites compared to 50% from the PB sites. In addition, evidence of predation due to moon snails, _Euspira_ spp., was noted only in CB (Table 2). Mean relative growth not only varied by 14% between embayments, but differed significantly between sites within each embayment (GC > LR by 29%, HE > HW by 37%; Table 4). Number of recruits varied between sites within CB (by 246%), but not in PB (Table 6).

Reasons for these differences in survival, growth, and recruitment within and between embayments and sites within embayments are speculative and based only on observations rather than quantitative measurements along some potentially important gradient (sensu Thrush et al., 2000). For example, at LR in PB, the distance between the upper and lower intertidal blocks was only 40 m, even though the length of time units were exposed at each tidal height was similar to the other sites. LR was the only site where mean survival was similar between tidal heights. In addition, although predation was important at LR, the difference in survival between open enclosures and protected units (pooled across tidal height and intraspecific density) was 17.8% compared to 35.8% at GC, approximately 1 km away. The LR site had few large boulders and no ledges either in the upper or lower intertidal. Conversely, at GC, extensive ledges covered with fucoid algae punctuated the soft-bottom landscape. Green crabs, a major predator of soft-shell clams (Ropes, 1968), seek temporary refuge from gulls (_Larus_ spp.) during low tide in this habitat (per. obs.), similar to their behavior in other rocky shore locations in New England (Bertness, 1999) and northern Europe (Thieltges et al., 2004). Although a small proportion of crushed individuals was discovered both at LR and GC (Table 2), perhaps crab predation is higher at GC than LR. If one assumes that clams missing from experimental units result from predators that either excavate and consume clams away from the units or crush the valves into fragments too small to be detected (Beal et al., 2001), then the higher missing rate of clams at GC may be attributed to greater crab and other benthic predators compared to LR.

Relative clam growth was slower and final mean SL smaller at LR vs. GC and HW vs. HE (Tables 4 and 5). One explanation for this result is that in both embayments, each flood tide passes over and across the easternmost site (GC and HE) before it reaches the westernmost site (LR and HW). Differential microalgal concentrations in the water column (e.g., Posey et al., 2002; Carmichael et al., 2004) could exist between the western vs. eastern sites within each embayment; however, chlorophyll a concentrations were not monitored. If sufficient numbers of benthic filter-feeders are

present at GC and HE, then perhaps the difference in growth between sites integrated over the experimental period occurred due to differential grazing at the benthic boundary layer (Fréchette and Bourget, 1985). Local depletion of suspended phytoplankton has been observed in populations of infaunal, suspension-feeding bivalves (Summerson et al., 1995; Montaudouin and Bachelet, 1996).

Given the survival results of cultured clams, it is not too surprising that the number of wild juveniles of *Mya* varied significantly at each spatial scale (Table 6). The observed size range of the recruits in November 2003 (1.4–8.2 mm SL) suggests that only the 0-yr class was represented (Beal and Kraus, 2002). Their relative density was 46% higher in CB than PB, and, except for LR, significantly higher numbers were found in upper vs. lower intertidal blocks (Fig. 6).

Significant spatial heterogeneity was observed for each dependent variable at the scale of the blocks that were located approximately 5 m apart within each site and tidal height. In each case, however, the heterogeneity occurred within the upper intertidal blocks that are most susceptible to daily and cumulative variations in air temperatures, runoff, and sedimentation because these tidal locations are exposed to air significantly longer during each tidal cycle. In addition, there is a greater likelihood of differences in micro- and macro-topographic features along the upper intertidal compared with the lower intertidal in many mud flats in this region (pers. obs.). For example, ice floes may scour sections of the upper intertidal during January and February creating small depressions that hold pools of seawater at low tide, or remove the smaller, lighter sediment fractions, or drop cobble and small boulders. Freshwater runoff after a significant rainfall can scour portions of the upper intertidal removing the upper few cm of muddy sediments exposing gravel or larger particle sizes. Conversely, the lower intertidal often appears as a featureless, flat surface throughout the year. Therefore, it is reasonable to use block designs to assess spatial variation especially in the upper intertidal of low energy mud flats where horizontal features may be heterogeneous. Sometimes, the heterogeneity may result in faster growth, especially if there are differences in submergence times between blocks. Causes of differences in survival between blocks may not be so obvious. For example, Beal et al. (2001) observed significant variation between blocks only 10 m apart in juvenile soft-shell clam survival in the upper intertidal at a site in eastern Maine, USA. The source of variation was due to atypically high mortalities caused by moon snails that foraged in some, but not all blocks.

4.2. Importance of predation and competition along the tidal gradient on clam survival and growth

This study contributes to a better understanding of the relative roles of predation and competition in controlling the intertidal abundance of juvenile clams in eastern Maine. In this region and elsewhere in the northeast US, there is a predominance of higher densities of 0- and 1-yr size classes of *Mya* near the upper and mid intertidal, and a paucity of animals near the low intertidal (Dow and Wallace, 1961; Matthiessen, 1963; Green and Hobson, 1970; pers. obs.). This may result from hydrodynamic forces of bedload transport (sensu Emerson and Grant, 1991; Hunt and Mullineaux, 2002) and differential predation along the tidal gradient (or an interaction between the two) similar to that observed by Beal (1994) and Beal et al. (2001) for cultured clams as well as in the two embayments in the present study (see Table 2 and Fig. 2). Predators such as benthic fish and large crustaceans can extend their foraging time by preying on these bivalves at locations lower on the shore where their risk of being preyed upon, especially by gulls, is reduced. This results in a spatial refuge for clams near the upper intertidal much like that described for periwinkles, *Littorina irrorata,* from blue crab, *Callinectes sapidus*, attack in two North Carolina, USA, salt marshes (Lewis and Eby, 2002). Similar refuges for the infaunal clam, *Mercenaria mercenaria*, exist between intertidal and subtidal sand bottoms in North Carolina (Micheli, 1996).

Differential recruitment patterns may be partly responsible for the observed distribution of small clams, however, evidence exists to the contrary. Fegley et al. (1996) found no consistent pattern of recent settlers of *Mya* at five eastern Maine intertidal flats along a tidal gradient from the upper to lower shore. In this study, the average difference in percent survival between upper and lower shore within open enclosures was nearly 20% ($\bar{X}_{High}$ vs. $\bar{X}_{Low} = 34.7 \pm 5.3\%$ vs. $29.2 \pm 5.4\%$, respectively; $n = 80$). If differences in clam survival between tidal heights observed here and at other tidal flats in this region are representative and temporally consistent, then predation could be invoked as the primary factor influencing the distribution and abundance of 0- and 1-year class individuals in the intertidal zone.

Although losses of juvenile clams during this study varied between embayments and between sites within PB, mean clam survival in open enclosures ($31.9 \pm 3.72\%$, $n = 160$; range $= 8.8–60.8\%$, Table 2) was lower than that observed over comparable time intervals using clams of a similar origin at other eastern Maine intertidal locations. For example, Beal and Kraus (2002) observed a 78.3%

survival rate of small *Mya* (initial SL=14.6 mm) in similar experimental units at stocking densities from 330 to 2640 m^{-2} from mid-April to early October 1991 at the mid-intertidal near Cutler, Maine. Exclusion of predators resulted in a 9% enhancement in that study whereas this level was 125% in the present study. Mean clam survival in open enclosures vs. protected units pooled over embayment, site, tidal height and blocks was 71.9±2.63% vs. 31.9±3.72%, *n*=160, and this difference accounted for 45% of the total variation in clam survival. Beal et al. (2001) observed an 85.6% survival of juveniles of *Mya* (pooled across stocking densities from 330 to 1320 m^{-2}) in open enclosures near the upper intertidal at a mud flat in Jonesport, Maine from early April to early December 1996. Predator exclusion resulted in a 10.2% enhancement in mean survival. Conversely, in the same study, clam survival in open enclosures near the low tide level was 54% compared to 86.8% in units protected with plastic, flexible netting (6.4 mm aperture), an enhancement of approximately 60%. Drawing conclusions about relative predation intensity in Cobscook and Passamaquoddy Bay compared to studies conducted 7–13 years earlier at intertidal sites 50–75 km west of those embayments may be problematic. However, by comparing changes in size-frequency distributions of *Mya* from 1977–1979 at a site in Cobscook Bay (Federal Harbor, Lubec, Maine), Commito (1982) inferred that mortality of wild clam juveniles (4–8 mm SL) was 96.5% year^{-1} for the first five years. Commito's observations, the field studies of Beal et al. (2001) and Beal and Kraus (2002), as well as data presented here for CB and PB, suggest that clam losses due to predators in these and other embayments are intense, especially during the first full growing season.

Increasing clam density from 660 to 1320 m^{-2} led to an overall mean increase in clam mortality of ca. 17% (*P*=0.0003, Table 3); however, this effect explained only 2% of the total variation in clam survival and apparently was unrelated to differences in handling or stress-related mortalities (see the dead undamaged categories of Table 2). If one assumes, however, that missing clams are due to predator foraging both in protected and open enclosures, then combining data from the percent missing and percent dead crushed/chipped columns of Table 2 results in an average difference between the two density treatments of 7.7%. Because approximately 20% of the clams were missing from completely protected experimental units, I assume that the flexible netting did not exclude predators completely, but simply deterred them. That is, the data suggest that predators foraged in a density-dependent manner regardless of level of protection. Similar results were observed by Beal et al. (2001), where the difference

over the same experimental densities was ca. 5%, but Beal and Kraus (2002) did not observe a similar low-density refuge for *Mya* over the experimental densities (see above) in that field trial. Other manipulative studies using adults of *Mya* in subtidal habitats of rivers emptying into Chesapeake Bay demonstrated that low density refuges exist on sandy bottoms (Seitz et al., 2001), which confirmed earlier laboratory trials (e.g., Lipcius and Hines, 1986; Eggleston et al., 1992).

Clams added new shell at an average of 0.08± 0.003 mm day^{-1} (*n*=303), or approximately 15.1± 0.49 mm during the 185 day experiment, but rates varied within and between embayments (Table 4). Because animals used in these field experiments were obtained from a single, unselected line of hatchery-reared individuals (pers. obs.), differences in growth between embayments and tidal heights (Fig. 5) are presumed unrelated to genetic control (sensu Bayne, 2004) but due to other factors. For example, tidal height explained approximately 35% of the variability in relative growth (Table 4). Relative growth varied inversely with tidal height at both sites within each embayment averaging approximately 30% and 70% faster in low vs. high intertidal blocks at the two PB and CB sites, respectively. This result was expected given the difference in immersion time between low and high intertidal blocks was 2–2.5 h tide^{-1}, and is similar to previous studies with juveniles and adults of *Mya* (Newcombe, 1935; Roseberry et al., 1991; Beal et al., 2001) and other infaunal suspension-feeding bivalves (Peterson and Black, 1987).

Neither increasing intraspecific clam density nor excluding predators had a statistically significant effect on relative growth or final SL. If density-dependent growth had been detected, it was likely to have occurred in the upper intertidal blocks at each site where microalgal resources may be limiting. This was not the case; however, relative growth of clams stocked at 1320 m^{-2} at three of four sites (LR, GC, HE) did average 5.8% less than growth of clams at the lower density (660 m^{-2}). This depression was similar to that observed by Beal et al. (2001) at the upper intertidal of a mud flat in Jonesport, Maine, but over a wider range of intraspecific juvenile clam densities (i.e., 330–1320 m^{-2}). No attempt was made in this study to control for the potential effect of the presence of protective netting on clam growth. Previous work with juveniles of *Mya* has demonstrated that relative growth and final mean SL in open enclosures vs. protected units is rarely different (Beal, 1994; Beal et al., 2001). Here, final mean SL of clams in open vs. protected units pooled across embayment, density, site, and tidal heights was 25.2±0.72 mm (*n*=74) vs. 24.5±0.74 mm (*n*=80), or <3% difference.

5. Conclusion

Previous field studies in the soft-bottom benthos that have examined bivalves, polychaetes, nemerteans, gastropods, and small crustaceans have demonstrated the relative importance of predation in regulating populations of juveniles or adults (Peterson, 1982a,b; Commito and Shrader, 1985; Richards et al., 1999; Bourque et al., 2001; Seitz et al., 2001; Posey et al., 2002). Here, approximately 45% of the variability in clam survival was explained by excluding predators from experimental units (Table 3). Although embayment (4%), tidal gradient (1.7%), density (2%), and sites within embayments (<1%) were all statistically significant (Table 3), these factors separately and combined pale in importance to predation in explaining variation in survivorship during this study. Adults of *Mya* are well-equipped to avoid predators because their relatively large size affords them a depth refuge from most consumers (Blundon and Kennedy, 1982; Seitz et al., 2001). During its juvenile phase, however, *Mya* is highly susceptible to both epibenthic and infaunal predators (Commito, 1982; Beal et al., 2001; Hunt and Mullineaux, 2002; this study) because it cannot burrow deeply enough to avoid encounters with most predators. Given the intensity of predation on juveniles of *Mya* observed here and in previous studies in this geographic region, an important question remains: how do sufficient numbers of soft-shell clam juveniles escape predation and reach a size where they are capable of reproducing at least once (which may take 2–4 years in eastern Maine; Ropes and Stickney, 1965) before they die? Numerous hypotheses, singly and in combination, can be invoked to answer this, including fast growth (Commito, 1982), heterogeneous habitats (Lipcius and Hines, 1986), low-density patches (Seitz et al., 2001), post-larval transport (Hunt and Mullineaux, 2002), and differential survival along a tidal gradient (Beal et al., 2001). Future work should concentrate on the relative roles that these factors play in limiting predation on juveniles of *Mya*.

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