Interactive effects of initial size, stocking density, and type of predator deterrent netting on survival and growth of cultured juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine

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Abstract

Recent declines in commercial harvests of soft-shell clams, *Mya arenaria* L., in Maine, USA, have prompted state and local officials to consider enhancing wild stocks with hatchery-reared seed. We conducted two manipulative field experiments in the soft-bottom intertidal zone during 1990–1991 in eastern Maine to assess effects of predation, intraspecific competition, and initial planting size on the survival and growth of cultured individuals of *Mya*. Experiment I (23 June 1990 to 13 June 1991) tested interactive effects of two planting sizes (small=8.5 mm shell length (SL); large=11.8 mm SL) and protective netting on fate and growth of clams. Animals of each size were added to separate experimental units within each of 60 1-m^2 areas delimited by a wooden box. To deter predators, 50 boxes were covered with a specific type of plastic netting that differed in aperture size (4.2, 6.4 and 12.8 mm) and degree of rigidity (flexible vs. extruded) while 10 boxes served as controls (without netting). Small clams grew at a faster rate than large clams, but both added approximately 18 mm of new shell by the end of the study. Growth was unaffected by netting size and rigidity, but 13% more clams were recovered alive after a year in protected vs. unprotected treatments (84% vs. 71%). Survival was independent of netting type. The presence of netting resulted in nearly a 3× enhancement of wild spat (<15 mm SL) compared to unprotected controls (568.8±24.4 vs. 199.6±22.8 m^{-2}). This result suggests that the decline of wild stocks in eastern Maine may not be related to recruitment failure, but to post-settlement events, such as predation, which remove clams from the intertidal. In Experiment II (15 April to 6 October 1991), clam (14.6±0.2 mm SL) density was manipulated across four levels from 333 to 2664 m^{-2} in protected (extruded netting, 12.8 mm aperture) and unprotected 1-m^2 boxes. Survival within unprotected boxes

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was independent of stocking density (79%), but was inversely density-dependent in protected boxes (77% in the lowest density treatment increasing to a mean of 88% in the other three treatments). A negative cubic relationship explained the effect of density on growth. We present the first mariculture strategy for public stock enhancement or private entrepreneurs interested in rearing *M. arenaria* in Maine and the northeast US. Hatchery-reared juveniles 8–10 mm SL should be planted in the spring near or below mid tide levels at densities between 333 and 666 m^{-2} and protected with flexible netting (6.4 mm aperture) raised several centimeters above the sediment surface. Netting should be removed from mud flats in the late fall before the threat of ice and severe winter storms. Animals should attain sizes between 25 and 30 mm SL during this time and reach a size refuge from burrowing and other predators. Growth to legal, commercial size (50.8 mm SL) should take another 2–4 years depending on geographic location and mean seawater temperature. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The ultimate goal of shellfish aquaculture, for private enterprise or public stock enhancement, is to maximize yield per unit of time, space, and capital invested. This can be accomplished by determining growth and survival responses of the culture candidate under different field conditions. Perhaps the most important parameters to investigate in this regard, and ones that are relatively easy to manipulate, are how stocking density and planting size influence growth and survival in the presence vs. absence of large predators (Eldridge et al., 1979; Walker, 1984, 1985; Kraeuter and Castagna, 1986; Britton, 1991; Spencer et al., 1991; Toba et al., 1992; Peterson et al., 1995; Summerson et al., 1995; Fernandez et al., 1999).

Typically, type III survivorship curves (Deevey, 1947) best describe mortality patterns in invertebrates such as bivalves with high age-specific fecundity schedules (Iribarne et al., 1995). Risk of predation generally decreases with increasing size/age primarily due to mechanical limitations of the predator or energy constraints imposed by handling and consuming large prey (Paine, 1976; Elner and Hughes, 1978; Sousa, 1993). For shellfish aquaculturists, determining the smallest plantable-size seed that will return highest yields depends on knowledge about local predators and what decreases their foraging efficiency (Arnold, 1984; Boulding and Hay, 1984; Sponaugle and Lawton, 1990; Mansour and Lipcius, 1991; Irlandi, 1994; Masski and Guillou, 1999; Nakaoka, 2000). Generally, there is a trade-off between effectiveness of predator deterrents such as cages, netting, gravel, shell, etc. and clam size because, in reality, these deterrents are not completely efficacious. Sometimes, they can be subverted by birds, burrowing predators or by predators small enough to enter the protected area that subsequently become entrapped by growing too large to escape (Walker, 1984; Kraeuter and Castagna, 1985; Peterson et al., 1995; Smith and Langdon, 1998; Cigarria and Fernandez, 2000). Since many predators forage selectively according to the size of their prey, smaller clams are more susceptible and, invariably, suffer greater mortality than larger animals planted in the same protected environments.

The use of plastic and other types of netting, for example, to deter predators of cultured clams has been the focus of much research (Kraeuter and Castagna, 1985; Walker and Heffernan, 1990; Spencer et al., 1992; Toba et al., 1992; Smith and Langdon, 1998; Fernandez et al., 1999). These, and other investigations where nets or netted cages have been used to exclude predators from populations of small, infaunal bivalves (Smith et al., 1955; Peterson, 1982b; Boulding and Hay, 1984; Skilleter and Peterson, 1994), have demonstrated significant size-specific survival enhancement in protected treatments. Many of these studies have highlighted the relationship between aperture size of protective mesh and clam size. Juveniles of most cultured bivalve species are highly mobile and, if the openings of the mesh are large enough, clams may emigrate and become more vulnerable to attack (Walker and Heffernan, 1990; Spencer et al., 1992).

The interaction between mesh size and clam size is critical both from field grow-out and hatchery perspectives. Because costs of cultured seed increase nonlinearly with size (Fig. 1), due primarily to the logistics of producing and handling large numbers of animals (<2 mm shell length, SL) under nursery conditions (T. Simmons, Muscongus Bay Sea Farm, Friendship, ME, personal communication), hatcheries are designed to produce large numbers of very small individuals. Clam farmers and communities engaged in stock enhancement must adopt a strategy to optimize field survival. Generally, the choice is a dichotomous one once seed have been purchased from a hatchery. Seed either are planted directly to field sites or grown to larger sizes in nurseries where they remain for several weeks to months before planting. This decision should be based on growth and survival rates of various sizes of seed from field trials as well as costs of seed and predator deterrents (e.g., Arnold, 1984; Malinowski, 1986; Hurley and Walker, 1993; Peterson et al., 1995).
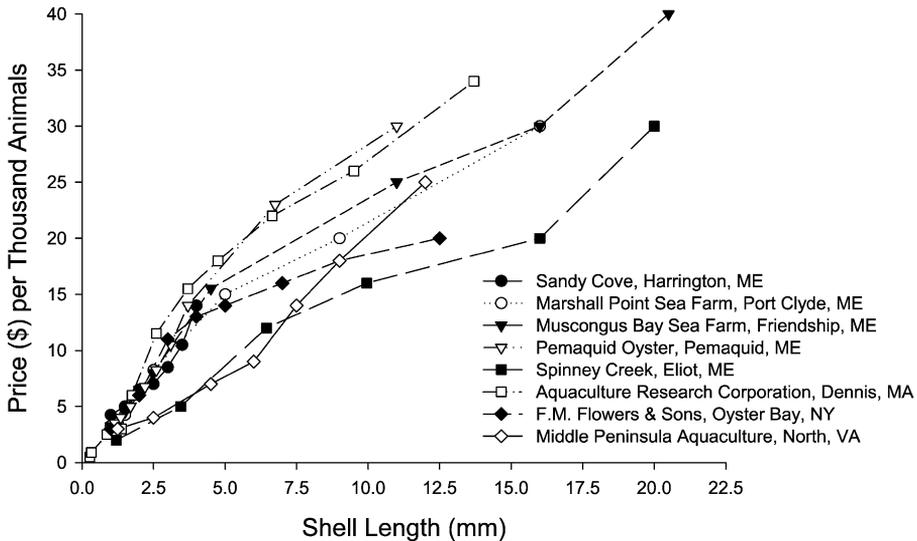

Fig. 1. Price−shell length (mm) relationship for eight shellfish hatcheries in the northeast US. Prices quoted as of 1 April 2001.

Another important choice shellfish aquaculturists must make involves seed stocking densities. A basic understanding of size-dependent crowding effects on growth and survival has practical applications because this information clearly is critical to decisions that individuals or communities must make when considering costs vs. future benefits of any aquaculture venture (Adams et al., 1991). Theoretically, population and individual growth rate of a given species declines with increasing intraspecific density (Begon et al., 1990) because resources such as space (interference competition) or food (exploitative competition) eventually become limiting. Density-dependent growth rate has been demonstrated in natural populations as taxonomically diverse as amphibians (Wilbur, 1980), mammals (Leberg and Smith, 1993), gastropods (Branch, 1975), and bivalves (Peterson, 1982a). These investigations are important to aquaculturists because they indicate that it is possible to deplete local sources of food at relatively low intraspecific densities. This suggests the importance of assessing effects of exploitative competition over a wide range of stocking densities (e.g., Summerson et al., 1995; Cigarria and Fernandez, 1998).

Laboratory and field investigations examining the effects of intraspecific density on survival of bivalves have shown at least three different outcomes are possible depending on the relationship between size of predator and prey and/or type of habitat. For example, increasing predation rate with increasing prey numbers (positive density-dependent response leading to a low-density refuge) has been demonstrated for crabs (Lipcius and Hines, 1986; Haddon et al., 1987; Iribarne et al., 1995) and eagle rays (Hines et al., 1997) preying on clams and crabs feeding on oysters (Eggleston, 1990a,b). Conversely, prey survival may actually increase over limited ranges of intraspecific densities (inverse density-dependence; Eldridge et al., 1979; Lipcius and Hines, 1986; Sponaugle and Lawton, 1990). Density-independent responses are also possible as in the case of whelks preying on clams (Peterson, 1982b) and crabs preying on cockles (Montaudouin and Bachelet, 1996; Masski and Guillou, 1999).

The majority of experimental fieldwork involving cultured clams has been directed towards shallow-burrowing, thick-shelled species in the family Veneridae (e.g., hard clams, *Mercenaria mercenaria* L., carpet-shell clams, *Venerupis decussata* (L.), and Manila clams, *Tapes philippinarum* [Adams and Reeves]) (Walker, 1984, 1985; Manzi and Castagna, 1989; Vaughn et al., 1989; Adams et al., 1991; Britton, 1991; Toba et al., 1992; Summerson et al., 1995; Hadley et al., 1997). These and other investigations have led to advances in nursery and field grow-out. Today, hard clams are farmed intensively in every state along the east coast of the US south of and including Massachusetts, but especially in the southeastern United States.

In Maine, USA, populations of the deep-burrowing, soft-shell clam, *Mya arenaria* L., are ubiquitous in soft-bottom, intertidal sediments (Hanks, 1963). Because the intertidal zone in Maine is considered a public resource, coastal communities adjacent to clamming habitat may opt to co-manage wild populations of *Mya* (Ellis and Waterman, 1998) with the state's Department of Marine Resources (DMR). Management schemes typically are based on a flat-by-flat assessment of standing stock followed by a decision whether to close or open the area to commercial harvesting (sensu Robinson and Rowell, 1990). The success of these management plans depends, primarily, on the strength of natural clam recruitment and subsequent survival of 0-year class individuals. Since 1984, when 2403

metric tons (t) of soft-shell clams were landed in Maine (worth $11.8 million), there has been a steady decline in coast-wide landings and standing stocks so that by 1999, only 43% of the 1984 levels were harvested (1035 t, worth $10.5 million; NMFS, 2001). This downturn in natural production has encouraged some Maine communities to turn their attention to using hatchery-reared seed for stock enhancement purposes (Beal, 1994; Wallace, 1997; Ellis and Waterman, 1998).

Previous fieldwork with cultured juveniles of *Mya* in eastern Maine (Beal, 1994; Beal et al., 2001) has shown that growth is highly seasonal (April–November) with more than half of the shell accretion between June and August. In addition, unprotected animals <10 mm in shell length (SL) suffer moderate to heavy losses (50–75%) within several months after seeding regardless of transplant density or whether they are planted in spring or late summer. Low-density refuges have been observed for unprotected animals >10 mm SL planted at stocking rates between 166 and 1332 m^{-2}.

Many of the tests conducted by Beal (1994) were short-term (2–3 months), but occurred during periods of heaviest predation pressure and did not assess fully the effects of excluding predators. Here, we describe two field experiments conducted in eastern Maine where plastic netting was used to exclude predators from cultured juveniles of *Mya* for periods of 6 months to a year. The first evaluated the interactive effects of type of netting (flexible vs. extruded), mesh size and clam size on growth and survival over a year. The second examined the effects of four stocking densities (333–2664 m^{-2}) on clams grown with and without protective netting. We include additional information about natural clam recruitment from both experiments that may help explain the decline of wild stocks and offer the first mariculture strategy for growing cultured soft-shell clams in Maine and the northeastern US.

2. Material and methods

2.1. Study sites

Two intertidal mud flats in eastern Maine, USA were selected for these investigations: Sammy's Cove (SC) in Jonesboro near the mouth of the Chandler River (44°37′ 47″N; 67°32′ 36″W) and Duck Brook Flat (DBF) in Cutler near Holmes Bay (44°41′ 13″N; 67°18′ 35″W). SC is a narrow, steeply sloping (ca. 15°) flat with a horizontal distance between the extreme upper and lower intertidal of 110 m. The upper intertidal is comprised of granite ledges covered with *Ascophyllym nodosum* (L.) Le Jolis grading into small diatom-covered boulders and then to a soft-bottom area that extends ca. 75 m to the shallow subtidal. Sediments at SC consisted of a sandy mud (sensu Folk, 1980) with a graphic mean±1 s.d. of 3.2±0.27 Φ (*n*=2). Salinities at this site ranged from 29 to 31 psu over the course of the experiment. Conversely, DBF is broad and expansive with a shallow slope (ca. 1°) extending horizontally 540 m from the shore to the extreme low water mark. The upper intertidal is comprised of small rocks and boulders that grade quickly to a mud flat that extends 500 m towards Holmes Bay. The mid zone of the flat is characterized by small, irregular-shaped beds of eelgrass, *Zostera marina* L. ranging in size from 120 to 350 m^2 (Beal, 1994). The lower mudflat is topographically featureless.

We established our experiments between the mid and low zone at DBF where sediments were similar to those at SC (graphic mean=3.4 ± 0.54 Φ, n=2) and salinities ranged between 28 and 30 psu during the study. Those portions of each flat where the experiments were conducted became exposed twice daily for approximately 30 min to 1 h on each low tide depending on lunar cycle. Neither site contained commercial quantities of soft-shell clams or marine worms, *Neanthes virens* Sars and *Glycera dibranchiata* Ehlers; therefore, no disturbance due to harvesting of either species occurred at either site during the experimental periods (B. Beal, personal observation).

2.2. Experiment I—Sammy's Cove (23 June 1990 to 13 June 1991)

This study was designed to test the interactive effects of clam size and type/size of predator deterrent netting on clam growth and survival. On 23 June 1990, 20 haphazardly placed cores (A=0.0187 m^2; depth=20 cm) were taken to establish initial densities of juvenile and adult clams. Samples were sieved using a 0.5 mm mesh and clams enumerated and measured (SL=greatest anterior–posterior distance) using vernier calipers to the nearest 0.1 mm. On that same date, 60 wooden (spruce) frames measuring $1\times1\times0.2$ m wide with wooden legs ($30\times3\times3$ cm) at each corner were forced into the sediments to a depth of 15 cm. Frames were arrayed in a 6×10 matrix with ca. 1.5 m spacing between adjacent rows and columns. Six round, plastic horticultural pots (15 cm diameter$\times$15 cm depth, henceforth referred to as experimental units) filled with ambient sediments were pushed 14 cm into the mud within each frame in a 3×2 array with approximately 60 cm spacing between columns and 40 cm between rows. We affixed a piece of 4.2 mm (aperture) flexible netting (10 cm wide$\times$35 cm long) around the circumference of each experimental unit with two rubber bands. When units were in the sediments, the netting protruded, like fencing, approximately 4 cm above the rim and ensured that the clams we added to each unit (see below) would not emigrate and that small wild clams would be deterred from migrating laterally into the units.

Each of the six experimental units within a wooden frame was stocked with 12 hatchery-reared soft-shell clams (ca. 666 individuals m^{-2}) produced at the nearby Beals Island Regional Shellfish Hatchery (BIRSH; 44°31′ 21″ N; 67°36′ 38″ W) in 1989 and held over the winter according to Beal et al. (1995). This density was approximately twice the ambient density of wild soft-shell clams at another intertidal flat in eastern Maine (Commito, 1982). We randomly assigned one of two sizes of clams to the experimental units. Three units received "small" clams (mean SL±1 SE=8.5 ± 0.084 mm, n=185) while the others received "large" clams (11.8 ± 0.146 mm SL, n=237). We employed five separate types of netting (Table 1) and a control (no netting) to test the importance of predation, type (flexible [F] vs. extruded [E]), and aperture size of netting (4.2–12.8 mm) on clam survival and growth.

Fifty of the wooden frames, henceforth called boxes, were randomly chosen and each were covered with a 1-m^2 piece of netting that was affixed to the top of each box with stainless steel staples or galvanized roofing nails, depending on net rigidity. This design resulted in each net being 4–5 cm above the clams in each experimental unit. Beal (1994) found that netting applied directly to sediments often interfered with feeding because netting prohibited clams from extending their siphons above the sediment–water interface

Table 1
Types and weights of plastic netting used in Experiment I[a]

Aperture size (mm)	Type	Mass (g m^{-2})	Price m^{-2}
4.2	Flexible	43.7	$0.602
6.4	Flexible	40.5	$0.506
12.8	Flexible	47.2	$0.597
6.4	Extruded	470.9	$2.987
12.8	Extruded	562.2	$3.875

[a] All netting are manufactured by InterNet, Minneapolis, MN 55428. Prices are as of 1 April 2001.

depending on their size and net aperture. In addition, nets in direct contact with the sediment often cause localized areas of anoxia, especially in muddy substrates. The remaining 10 boxes were left uncovered and served as controls to assess the overall importance of predators in this system. Although the study site was revisited periodically during the next 12 months, no attempt was made to remove algae (mainly *Desmerestia* spp. and *Devaleraea ramentaceum* [L.]) that fouled the netting, especially the 4.2 mm flexible mesh.

On 13 June 1991, 20 benthic cores were taken in the area of the matrix and processed as described above. On that same date, all 360 experimental units were excavated, placed separately into labeled plastic bags, and taken to the University of Maine at Machias (UMM) where the contents of each was sieved using a 0.5 mm mesh. Clams were counted and assigned to one of four fate categories: alive, dead with undamaged valves, dead with chipped or crushed valves, and missing. Three linear SL measurements were recorded for each live clam. The first was delimited by a disturbance line that coincided with planting date (Beal et al., 1999) while the second was a distinct winter check representing cessation of growth in late fall (Beal, 1994). The final measure was total SL. In addition to hatchery-reared clams, natural spat (<15 mm SL) that had settled into the units during the experimental interval were counted and measured in two linear shell dimensions: SL at the distinct winter check and final SL. When the winter check was ambiguous (572 of 3064 occasions), only total SL was measured.

2.2.1. Statistical analyses—Experiment I

Although we collected data on several fate categories, we only analyzed statistically the survival data since additional analyses on, for example, numbers missing or dead crushed, would not be independent of the first analysis as total number of animals per experimental unit was constant. Survival data (number of live individuals in each experimental unit) was not normal and variances were heterogeneous ($P<0.05$). This was improved ($P>0.05$) after a Box–Cox transformation (Sokal and Rohlf, 1995) was applied. The field layout was a type of split-plot design (Steele and Torrie, 1980; Underwood, 1997), and, as such, the analysis contains both factorial (crossed) as well as nested elements. Analysis of variance (ANOVA) was performed using the following linear model:

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C(B)_{k(j)} + AC(B)_{ik(j)} + e_{l(ijk)}$$

where: Y_{ijkl} = transformed count of number alive within each experimental unit; μ = theoretical mean; A_i = clam size (small; large); B_j = type of protection (open; 4.2 F; 6.4 F; 12.8 F; 6.4 E; 12.8 E); C_k = box (1, 2,... 9, 10); and e_l = experimental error — a measure of variation that exists among observations on experimental units treated alike.

Several a priori, single-degree-of-freedom contrasts for the type of protection source of variation were of interest. These were:

1. Unprotected vs. protected (i.e., absence vs. presence of netting);
2. Flexible vs. extruded;
3. 4.2 F vs. the mean of the other two flexible types of netting;
4. 6.4 F vs. 12.8 F; and,
5. 6.4 E vs. 12.8 E.

When more than one contrast is performed, the type I error rate for the joint probability of the independent outcomes is equal to $(1-[1-\alpha]^r)$, where r is the number of contrasts. For example, the probability of making one or more type I errors would be 0.23 if five joint decisions are made at α=0.05. To reduce this experimentwise error rate, Winer et al. (1991) suggest adjusting the alpha level for each independent test using $\alpha' = 1-(1-\alpha)^{1/r}$. We also partitioned the source of variation due to box nested within type of protection into six orthogonal components, but, unlike the a priori contrasts, we did not adjust the type I error rate for two reasons. First, the overall sum of squares for this source of variation is the sum of squares from the six separate model II one-way ANOVA's (one for each protection treatment) that could have been examined independent of the larger ANOVA (Neter et al., 1990). Second, the variation from box to box within a given type of netting treatment is a random effect and, as such, we had no a priori knowledge about these effects. Partitioning these sums of squares allowed us additional information about heterogeneity among replicates within a given netting treatment.

$$\text{Relative growth (rg) : ([final length − initial length]/initial length)} \times 100\%$$

was calculated for each live clam and the mean rg for each experimental unit analyzed using the same linear model as described above. These data were normal ($P>0.05$; Shapiro–Wilks test; SAS, 1988) and variances homogeneous (Cochran's test; $P>0.05$); however, 10 of the 360 experimental units contained no live clams in June 1991, making the data unbalanced. We took the advice of Shaw and Mitchell-Olds (1993) who suggest the type III SS (SAS, 1988) be used to test each hypothesis in the ANOVA rather than the type I SS or replacing the missing values with means and adjusting the error degrees of freedom (Steele and Torrie, 1980).

To assess whether clam size or type of protection affected number of live spat at the end of the experiment, an ANOVA (linear model as described above) was performed on the square root of the number per experimental unit. This transformation normalized the data and homogenized variances ($P>0.05$). A priori contrasts and type I error rate adjustment for both rg and spat data were the same as those described above.

2.3. Experiment II—Duck Brook (15 April to 6 October 1991)

This field study was designed to test interactive effects of stocking density and predator exclusion on clam (mean SL=14.6±0.182 mm; n=100) survival and growth. On 15 April 1991, 16 1-m^2 wooden boxes, forming a 2×8 matrix with 2 m spacing between adjacent rows and columns, were pushed 15 cm into the sediments. Eight sediment-filled plastic horticultural pots (experimental units as described above), with strips of 4.2 mm flexible netting affixed to the perimeter of each, were forced into the sediments in each box in a 4×2 array. Clams, obtained from BIRSH, were added to experimental units at one of four densities (6, 12, 24, and 48 representing ca. 333, 666, 1332, and 2664 clams m^{-2}, respectively) so that two replicates of each density treatment occurred within each box. To exclude large predators, a 1-m^2 piece of 12.8 mm extruded netting (Table 1) was affixed to the top of eight randomly chosen boxes with galvanized roofing nails.

Experimental units were excavated from each box on 6 October 1991, placed separately into labeled plastic bags, and taken to UMM where the contents of each was washed through a 0.5 mm mesh. Cultured clams from the experiment were enumerated and placed into one of five fate categories: live, dead with undamaged valves, dead with crushed or chipped valves, dead with a countersunk bore hole, and missing. Two linear shell dimensions were taken for each live clam: a distinct mark associated with the time of planting and its final SL. We calculated rg for each live clam and assessed statistically mean rg per experimental unit.

As in the previous test, 20 benthic cores (A = 0.0187 m^2; depth = 20 cm) were taken on the day the experiment was initiated and ended to quantify number of wild adult and juvenile soft-shell clams. Samples were processed as described above.

2.4. Statistical analyses—Experiment II

Survival data were analyzed by ANOVA after an arcsine $P^{0.5}$ transformation (where P = mean proportion of live individuals per experimental unit at the end of the experiment) was used to correct for departures from normality and variance homogeneity ($P > 0.05$). The linear model was similar to that of Experiment I:

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C(B)_{k(j)} + AC(B)_{ik(j)} + e_{l(ijk)}$$

where: Y_{ijkl} = the arcsine-transformed percent alive within each experimental unit; μ = theoretical mean; A_i = intraspecific density (333, 666, 1332, 2664 m^{-2}); B_j=type of protection (protected or unprotected); C_k = box (1, 2,... 7, 8); e_l = experimental error.

Three mutually independent and orthogonal contrasts were employed to better understand the effect of increasing intraspecific density on clam survival. These were:

1. 333 m^{-2} vs. mean of the other three densities,
2. 666 m^{-2} vs. (1332 and 2664 m^{-2})/2,
3. 1332 vs. 2664 m^{-2}.

Because these are hypotheses developed prior to examining the results of the ANOVA, they are performed regardless whether the overall effect due to density is significant. Also, a priori contrasts can be used to examine details of interactive factors by decomposing these sources of variation into single degree-of-freedom tests (Winer et al., 1991) that allows one to interpret complex, higher-order interactions in a biologically meaningful manner (Underwood, 1997). Type I error rate for the three orthogonal contrasts was adjusted (as above).

ANOVA was performed on the untransformed mean rg because data were normal and variances homogeneous ($P > 0.05$). To determine the shape of the density response surface, a trend analysis (Winer et al., 1991) was performed that allowed us to distinguish between linear, quadratic, and cubic models. These a priori, single-degree-of-freedom tests are a type of orthogonal contrast and therefore require similar type I error rate adjustment ($\alpha' = 0.0169$).

Estimates of variation associated with all means are presented as standard errors (SE) unless otherwise noted.

3. Results

3.1. Experiment I

3.1.1. Survival

Clam survival from June 1990 to 1991 was generally high (>60%) across all treatment combinations (Table 2). Large clams had an average 7.8% higher survival rate than small clams pooled across all treatments ($85.6 \pm 2.39\%$ vs. $77.8 \pm 2.54\%$; $n=60$; $P < 0.0001$). The source of variation due to type of protection was significant ($P < 0.05$), but the orthogonal contrasts indicated that survival rates were similar among the 50 boxes covered with protective netting (Table 3). That is, predators were equally deterred regardless of

Table 2

Mean percent (± 1 SE) of each of four fate categories associated with cultured juveniles of *M. arenaria* from Experiment I (Sammy's Cove, Jonesboro, ME: 21 June 1990 to 13 June 1991)

Clam size	Type of protection	Alive	Dead undamaged	Dead crushed	Missing
Small	Unprotected	63.9 (4.9)	2.5 (0.9)	9.2 (3.3)	24.4 (3.7)
Small	4.2 Flexible	77.2 (5.3)	2.2 (0.8)	6.4 (2.3)	14.2 (4.1)
Small	6.4 Flexible	82.5 (3.6)	3.3 (1.2)	6.7 (2.7)	7.5 (1.7)
Small	12.8 Flexible	82.5 (3.0)	3.1 (0.9)	5.0 (2.3)	9.4 (2.3)
Small	6.4 Extruded	87.5 (2.6)	3.1 (1.0)	4.2 (1.9)	5.3 (1.4)
Small	12.8 Extruded	73.1 (6.1)	7.8 (3.1)	5.0 (2.5)	14.2 (4.3)
Large	Unprotected	77.8 (2.5)	1.9 (0.8)	4.7 (1.1)	15.6 (2.1)
Large	4.2 Flexible	82.2 (5.4)	2.2 (0.8)	5.6 (2.4)	10.0 (3.4)
Large	6.4 Flexible	90.8 (2.2)	1.4 (0.7)	3.6 (1.1)	4.2 (1.4)
Large	12.8 Flexible	87.2 (3.2)	0.8 (0.5)	3.1 (1.4)	8.9 (3.2)
Large	6.4 Extruded	88.9 (3.4)	4.4 (2.6)	3.3 (1.7)	3.3 (0.9)
Large	12.8 Extruded	86.9 (4.7)	0.8 (0.5)	5.8 (3.5)	6.4 (2.5)

Small $= 8.5 \pm 0.084$ mm; Large $= 11.8 \pm 0.145$ mm. Refer to Table 1 for description of plastic netting ($n = 30$).

mesh size and whether nets were rigid or flexible. The presence of the netting, however, enhanced survival of both sizes of clams by 13% ($P < 0.01$; Table 3). Mean survival in boxes without protective netting was $70.8 \pm 2.58\%$ ($n=10$) compared to $83.8 \pm 2.64\%$ ($n=50$) in protected boxes. The source that explained the largest percent (40.4%) of total variation in ANOVA was box (type of protection) ($P < 0.0001$; Table 3). Partitioning this source of variation into its six 9 degree-of-freedom components demonstrated that only the controls behaved in a truly homogeneous manner (Fig. 2). Increased variation in survival rate among boxes within a given type of netting treatment can be attributed mainly to the effects of crushing predators that were not completely excluded by the protected boxes. The high rates of mortality in some protected boxes (45–97%; Fig. 2) were associated with highest rates of clams recovered dead with crushed or chipped valves. Inspection of growth and disturbance lines on the surface of those damaged shells indicated that most of the predation events occurred sometime between April and June 1991 because the chipped shell margins occurred after the late fall/winter growth cessation check.

Nearly 25% of the small clams and 16% of the large clams in the unprotected boxes were missing. In addition, mean percent missing was $\geq 10\%$ for clams of both sizes

Table 3
ANOVA results on survival data from Experiment I

Source of variation	df	SS	MS	F	Pr >F
Clam size	1	2374.99	2374.99	24.6	0.0001
Type of protection	5	5311.57	1062.31	2.4	0.0476
Unprotected vs. protected	1	4851.90	4851.90	11.0	0.0016
Flexible vs. extruded	1	93.34	93.34	0.2	0.6468
Flexible: 4.2 mm vs. rest	1	68.52	68.52	0.2	0.6946
Flexible: 6.4 vs. 12.8 mm	1	58.60	58.60	0.1	0.7165
Extruded: 6.4 vs. 12.8 mm	1	239.21	239.21	0.5	0.4640
Clam size×type of protection	5	332.85	66.57	0.7	0.6336
Box (type of protection)	54	23,743.37	439.69	4.9	0.0001
Unprotected boxes	9	1160.54	128.94	0.9	0.5083
Flexible: 4.2 mm	9	6998.69	777.63	7.9	0.0001
Flexible: 6.4 mm	9	1983.87	220.43	2.1	0.0435
Flexible: 12.8 mm	9	3465.26	385.03	4.5	0.0002
Extruded: 6.4 mm	9	4131.99	459.11	7.3	0.0001
Extruded: 12.8 mm	9	6003.02	667.00	6.4	0.0001
Clam size×box (protection)	54	5214.22	96.56	1.0	0.3671
Error	240	21,770.30	90.71		
Total	359	58,747.30			

Data were transformed using the Box–Cox method where $\lambda = 3.10$ and the geometric mean (Π) of number alive per pot was 9.6. An adjusted type I error rate (α') of 0.0102 was used for each of the five single-degree-of-freedom orthogonal contrasts ($n=3$).
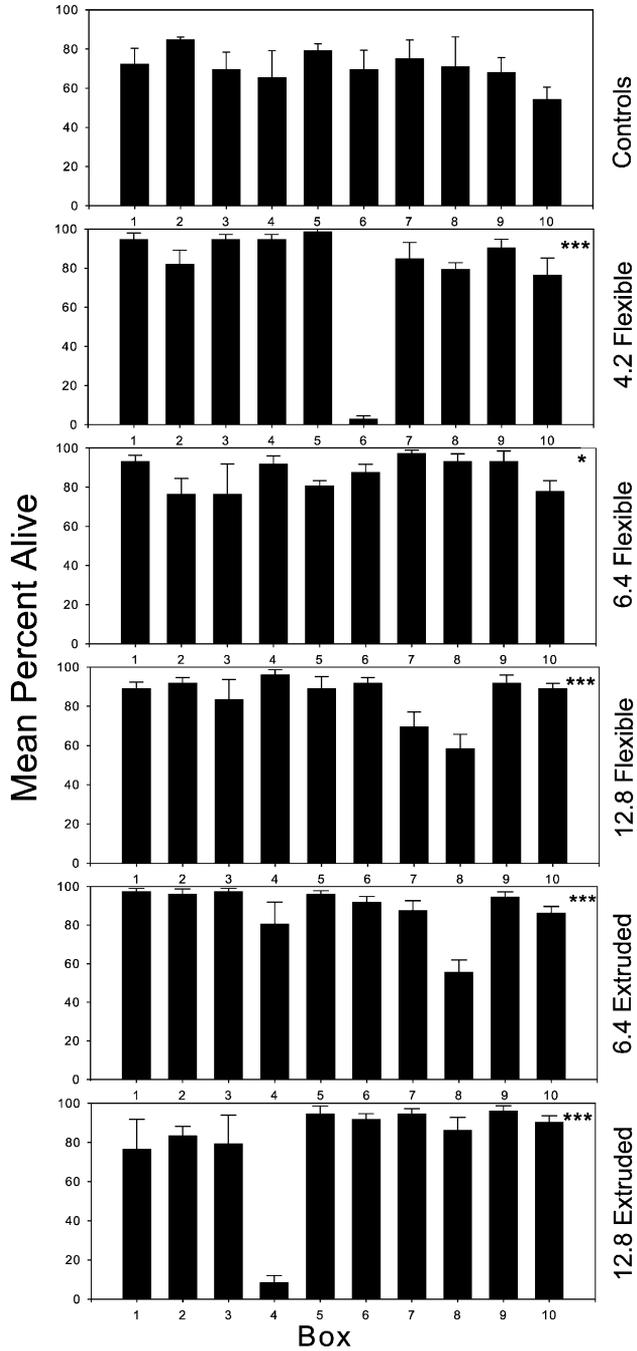
Table 4
ANOVA results on the untransformed relative growth rate data from Experiment I

Source of variation	df	SS	MS	F	Pr>F
Clam size	1	23.17	23.17	566.6	0.0001
Type of protection	5	0.61	0.12	1.2	0.3415
Unprotected vs. protected	1	0.41	0.41	3.9	0.0546
Flexible vs. extruded	1	0.00	0.00	0.0	0.9512
Flexible: 4.2 mm vs. rest	1	0.05	0.05	0.5	0.5039
Flexible: 6.4 vs. 12.8 mm	1	0.14	0.14	1.3	0.2583
Extruded: 6.4 vs. 12.8 mm	1	0.01	0.01	0.1	0.8289
Clam size×type of protection	5	0.23	0.05	1.1	0.3603
Box (type of protection)	54	5.71	0.11	2.9	0.0001
Unprotected boxes	9	1.27	0.14	1.6	0.1561
Flexible: 3.2 mm	9	0.63	0.07	0.5	0.8399
Flexible: 6.4 mm	9	0.48	0.05	0.4	0.9173
Flexible: 12.8 mm	9	0.28	0.03	0.3	0.9832
Extruded: 6.4 mm	9	0.15	0.02	0.1	0.9987
Extruded: 12.8 mm	9	2.90	0.32	2.7	0.0089
Clam size×box (protection)	54	2.21	0.04	1.1	0.2625
Error	230	8.30	0.04		
Total	349	42.22			

Ten of the 360 pots contained no live clams at the end of the experiment (13 June 1991) resulting in unbalanced data. Type III sums of squares were used in all hypothesis tests (Shaw and Mitchell-Olds, 1993). An adjusted type I error rate (α') of 0.0102 was used for each of the five single-degree-of-freedom orthogonal contrasts ($n=3$).

within boxes protected by the smallest netting and for small clams in boxes protected by the 12.8 mm extruded netting (Table 2). Sediment from two boxes in particular had been scoured somewhat so that entry by crabs or benthic fish most likely had been occurring for some time. Clams missing from experimental units were presumed victims of predation, although we cannot rule out the possibility that wave action washed some of the animals from the experimental units. Lateral emigration was restricted not only by the presence of the rigid plastic lip of each experimental unit, which extended 1 cm from the sediments, but also by the additional 4.2 mm netting that acted like a vertical fence and extended another 4 cm vertically above the margin of each unit.

3.1.2. Growth

Small clams grew 32% faster than large clams ($P<0.001$, Table 4). By June 1991, small clams had more than tripled their initial size (mean rg=220.4±1.95%, $n=172$) attaining an average of 26.9±0.15 mm SL whereas large clams more than doubled their initial size (mean rg=166.6±1.32%, $n=178$) attaining an average of 30.4±0.15 mm SL. Beal (1994) and Beal et al. (2001) have shown that shell growth of cultured juveniles of *Mya* in eastern Maine ceases late in the fall and recommences early the following spring. The period when shell growth slows or stops is accompanied by an obvious line (winter check) that we used

Fig. 2. Variation in mean percent alive (+1 SE) for small (8.5 mm SL) and large (11.8 mm SL) hatchery-reared soft-shell clams from box-to-box within each type of protected netting treatment and unprotected controls on 23 July 1991 at Sammy's Cove, Jonesboro, ME, USA. ANOVA indicated that variation was significant ($P<0.05$) in all but the control group. *($P<0.05$), ***($P<0.001$) ($n=6$).
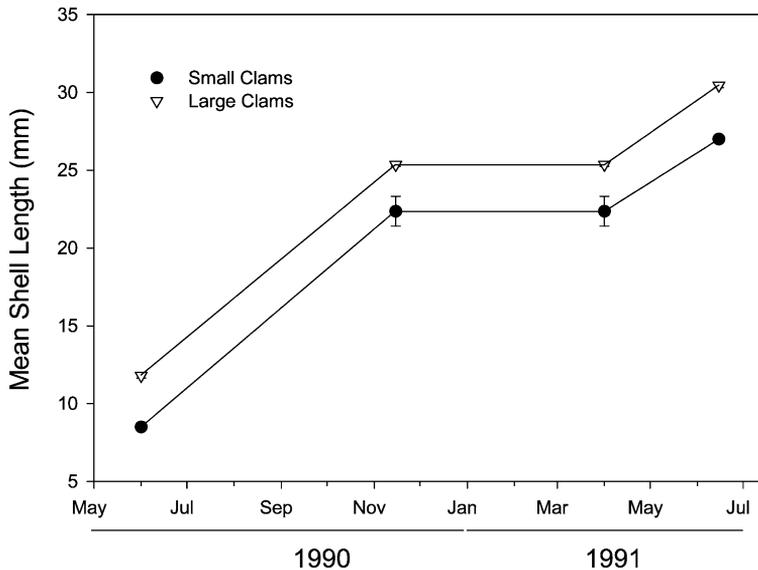
Fig. 3. Mean SL (±1 SE) of small (8.5 mm) and large (11.8 mm) hatchery-reared soft-shell clams at Sammy's Cove, Jonesboro, ME, USA. In eastern Maine, *M. arenaria* cease accreting shell from late October to the following April (Beal, 1994). SLs representing the fall/winter growth cessation were taken from live animals on 13 June 1991 by measuring the length of a distinct band (Newcombe, 1935) between the initial size marker (Beal et al., 1999) and ventral margin. Points representing fall/winter and final SL for each size class represent mean size of all live clams within each experimental unit. ($n_{large}=178$; $n_{small}=172$).

to estimate the relative proportion of shell added from 23 June 1990 (beginning of Experiment I) to late fall 1990, vs. the amount of growth that occurred between April and June 1991. For small and large clams, $74.9\pm0.10\%$ ($n=172$) and $72.9\pm0.11\%$ ($n=178$), respectively, of the yearly growth occurred in 1990 (Fig. 3).

Type of protection had no effect on rg (Table 4; Fig. 4). When sizes of clams were pooled, animals within in protected boxes grew nearly 6% faster than those in open boxes, but this difference was not significant ($P=0.054$, Table 4). Clams in all protected treatments behaved similarly except those in the 10 boxes with 12.8 mm extruded netting ($P=0.0089$, Table 4). A Student–Neumann–Keuls (SNK) test was performed to determine which box(es) had behaved differently and demonstrated that mean relative clam growth in 9 of the 10 boxes varied between 180% and 220%. Mean growth in the other was only 120%. Of the 72 clams added to the six experimental units in that box in June 1990, only six survived to the end of the experiment (box 4, 12.8 mm extruded, Fig. 2). Eighty percent of the growth of those six clams had occurred during 1990, suggesting that events that tended to remove clams from the experimental units (e.g., predation, scouring) may have resulted in slower growth rates between April and June 1991.

3.1.3. Benthic sampling and wild spat

Seven clams (19.44 ± 7.29 m^{-2}, $n=20$) were found during the June 1990 sampling. Mean shell length was 8.4 ± 2.58 mm and sizes ranged from 5.2 to 17.0 mm SL. In June
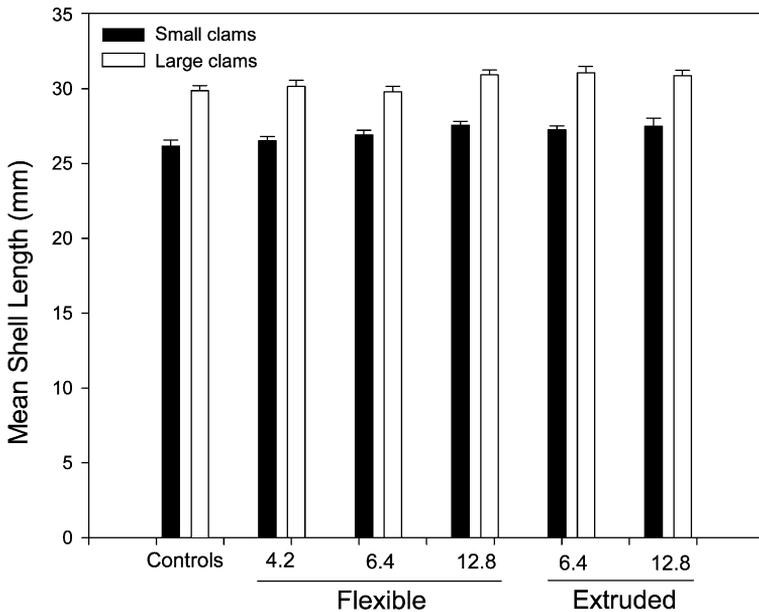
Fig. 4. Final mean SL (+1 SE) for small (8.5 mm) and large (11.8 mm) hatchery-reared clams on 13 June 1991 in protected and unprotected (control) boxes at Sammy's Cove, Jonesboro, ME, USA. ANOVA indicated that small clams grew approximately 32% faster than large clams, but the absolute amount of shell accreted in both groups was ca. 18.5 mm. No effects on mean growth due to presence, type, or size of netting was detected. Numeric values along the x-axis represent greatest aperture of plastic netting. See Table 1 for definitions of flexible and extruded. (n varies from 26 to 30).

1991, 62 clams (172.22 ± 17.48 m^{-2}, $n = 20$) with a mean SL of 7.1 ± 2.08 mm (range = 3.2–12.8 mm) occurred in samples. On both dates, clams from the benthic cores apparently were animals that had settled the previous fall because each had a distinct mark in the shell indicating a period of growth cessation.

A total of 3349 spat were recovered from the 360 experimental units in June 1991, but because some were damaged either in transport from the flat, or during the washing or measuring process, the number of clams measured to determine SL at the winter mark was 2492 whereas the maximum shell lengths of 3064 animals were taken (Fig. 5). Mean SL of clams at the time of the winter mark was 3.1 ± 0.02 mm (range = 1.1–9.1 mm) compared to the mean SL of animals in June 1991 (7.6 ± 0.05 mm; range = 1.6–15.0 mm).

The effect of excluding predators on numbers of wild spat was highly significant (Table 5; Fig. 6). Mean number of wild spat in experimental units within unprotected boxes was 3.7 ± 0.36 or 199.6 ± 22.82 m^{-2} ($n = 10$). The presence of protective netting resulted in nearly a three-fold enhancement of wild spat, as mean number per unit within protected boxes was 10.6 ± 0.46 or 568.8 ± 24.36 m^{-2}. Orthogonal contrasts indicated a differential enhancement effect across the various types of protective netting (Table 5). Greatest enhancement of wild spat occurred in boxes protected by nets with an aperture ≥ 6.4 mm ($P = 0.0054$, Table 5). Nearly twice as many spat were found in boxes with an aperture
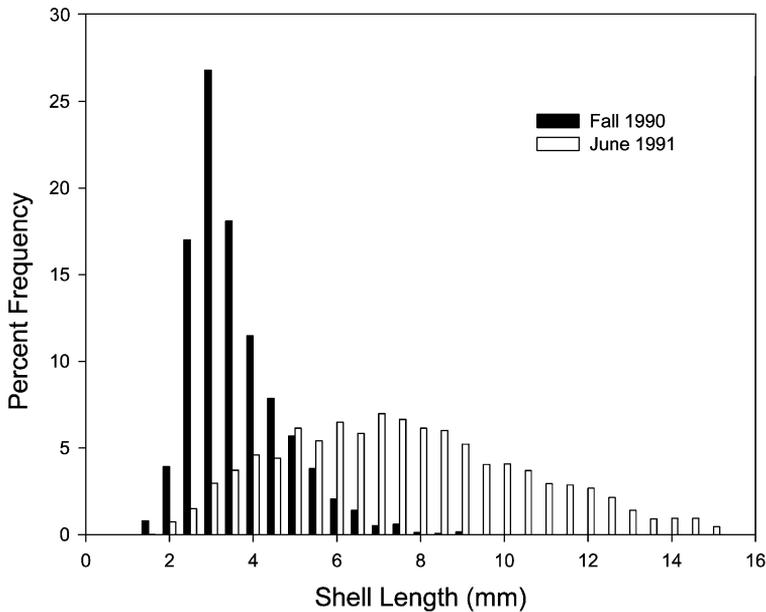
Fig. 5. Size frequency distribution of wild individuals of *M. arenaria* (spat) recovered alive ($N = 3349$, of which $n = 3064$ were measured) on 13 June 1991 pooled across all boxes at Sammy's Cove, Jonesboro, ME, USA. Size during winter ($n = 2492$) was inferred by measuring a distinct disturbance band or growth cessation line in the shell between the umbo and ventral margin (Newcombe, 1935).

≥ 6.4 mm (629.4 ± 28.45 m^{-2}, $n = 40$) compared to those protected with 4.2 mm flexible netting (326.0 ± 26.13 m^{-2}, $n = 10$).

Mean density of wild spat from experimental units within open boxes was not significantly different from mean density from the benthic cores taken near the experimental matrix area on 13 June 1991 ($t = 1.05$, $df = 78$, $P > 0.05$). This suggests that the presence of the boxes by themselves did not enhance wild spat densities, but that the observed enhancement was due primarily to the protective netting.

3.2. Experiment II

3.2.1. Survival

Survival exceeded 75% in all treatment combinations (Table 6). Mortality directly attributable to crustacean and gastropod predators was observed, but, in all cases, this amounted to <10% (Table 6). Clams missing from experimental units were likely removed by predators and consumed elsewhere or consumed in the unit but valves were crushed into pieces that were not sampled efficiently. When missing clams are added to the other two predator-related fate categories (dead crushed and dead drilled, Table 6), predation within unprotected boxes resulted in the loss of approximately 10–20% of animals. In protected boxes, this rate was 4–19%. Approximately 5% of clams (pooled over all treatments) were found dead with undamaged valves. Since this rate did not appear related

Table 5
ANOVA results on the square root-transformed number of live soft-shell clams ≤15.0 mm SL (spat) found within experimental units in Experiment I (Sammy's Cove, Jonesboro, ME) on 13 June 1991

Source of variation	df	SS	MS	F	Pr >F
Clam size	1	0.11	0.11	0.2	0.7003
Type of protection	5	141.30	28.26	37.2	0.0001
Unprotected vs. protected	1	82.13	82.13	25.6	0.0001
Flexible vs. extruded	1	15.13	15.13	4.7	0.0342
Flexible: 3.2 mm vs. rest	1	26.98	26.98	8.4	0.0054
Flexible: 6.4 vs. 12.8 mm	1	3.01	3.01	0.9	0.3362
Extruded: 6.4 vs. 12.8 mm	1	14.05	14.05	4.4	0.0410
Clam size×type of protection	5	1.49	0.29	0.1	0.9930
Box (type of protection)	54	173.07	3.20	4.2	0.0001
Unprotected boxes	9	12.19	1.36	2.3	0.0294
Flexible: 3.2 mm	9	11.00	1.22	2.3	0.0335
Flexible: 6.4 mm	9	50.08	5.56	5.5	0.0001
Flexible: 12.8 mm	9	21.41	2.37	4.3	0.0004
Extruded: 6.4 mm	9	58.73	6.53	7.4	0.0001
Extruded: 12.8 mm	9	19.66	2.18	3.3	0.0030
Clam size×box (protection)	54	28.16	0.52	0.7	0.9509
Error	240	182.57	0.76		
Total	359	526.70			

Type I error rate was adjusted to $\alpha' = 0.0102$ for each of the five single-degree-of-freedom orthogonal contrasts ($n = 3$).

either to level of protection or stocking density (Table 6), this mortality may have been due to stress from handling. If this hypothesis was correct, we assume that death of these 128 individuals within $n = 46$ experimental units would have occurred soon after clams were seeded and, therefore, initial (April = 14.5 ± 0.30 mm) and final (October = 16.3 ± 0.49 mm) mean SLs of dead clams with undamaged valves should be statistically indistinguishable. Mean SL was significantly different ($t = 4.49$, $df = 45$, $P < 0.0001$) between these two groups, indicating that, in general, clams grew approximately 12% of their initial length before dying.

Although the main effects of excluding predators and stocking densities were not significant, there was a significant protection×density interaction ($P = 0.0425$, Table 7). One of three orthogonal contrasts associated with the interaction source of variation was significant ($P < 0.01$) and indicated that the relationship between clam survival in the lowest vs. those in the three highest density treatments differed depending whether or not animals were protected from predators. For example, in unprotected boxes, there was no effect due to stocking density (333 m^{-2} = $80.2 \pm 2.01\%$ [$n = 16$] vs. combined mean of remaining three density treatments = $77.9 \pm 2.36\%$, [$n = 48$]). However, there appeared to
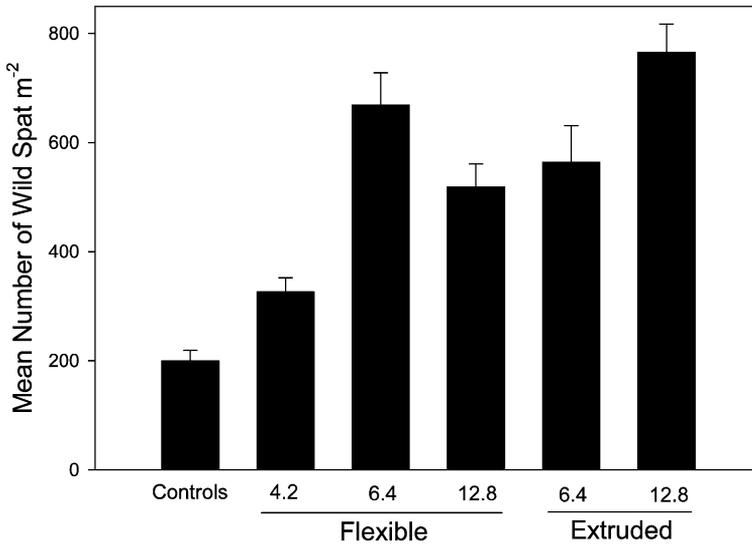
Fig. 6. Number of wild juveniles of *M. arenaria* m^{-2} (+1 SE) recovered alive within experimental units inside boxes at Sammy's Cove, Jonesboro, ME, USA on 13 June 1991. ANOVA indicated an approximate three-fold enhancement of spat numbers in protected vs. unprotected boxes. In addition, significantly more spat were found in boxes protected with netting ≥6.4 mm aperture (Table 5). See Fig. 4 for description of x-axis labels ($n = 10$).

be an enhancement in clam survival due to increasing density in protected boxes (333 m^{-2} = 77.1±6.61% [$n = 16$] vs. combined mean of remaining three density treatments = 88.4±6.49% [$n = 48$]). As in Experiment I, we found a significant box (protection) effect (Table 7); however, when this source of variation was partitioned, only survival in unprotected boxes was highly variable. For example, the range of mean survival rates within unprotected boxes was 31.7% whereas the range within boxes covered with netting was 18.7%.

Table 6

Mean percent (±1 SE) of each of five fate categories associated with cultured juveniles of *M. arenaria* from Experiment II (Duck Brook Flat, Cutler, ME: 15 April to 6 October 1991)

Number m^{-2}	Protection	Alive	Dead undamaged	Dead crushed	Dead drilled	Missing
333	Unprotected	79.2 (7.2)	9.4 (5.0)	5.2 (2.9)	1.0 (1.0)	5.2 (1.9)
666	Unprotected	76.6 (5.8)	6.8 (3.5)	7.8 (3.8)	0.0 (0.0)	8.9 (2.8)
1332	Unprotected	77.6 (3.7)	2.1 (0.8)	8.3 (2.9)	0.5 (0.5)	11.5 (2.2)
2664	Unprotected	79.6 (2.3)	2.3 (0.9)	2.9 (1.0)	1.2 (0.8)	13.9 (2.3)
333	Netting	76.0 (7.3)	5.2 (2.5)	3.1 (1.7)	9.4 (6.8)	6.3 (2.6)
666	Netting	86.5 (3.9)	6.3 (2.3)	2.6 (2.1)	0.5 (0.5)	4.2 (1.5)
1332	Netting	91.9 (1.5)	3.9 (1.4)	0.5 (0.4)	1.0 (0.6)	2.6 (0.9)
2664	Netting	86.7 (4.3)	3.5 (1.7)	2.6 (1.1)	0.4 (0.4)	6.8 (1.9)

Number m^{-2} refers to stocking density of clams within experimental units ($A = 0.0187$ m^2). Initial mean SL of clams = 14.6±0.18 mm. Netting was extruded with an aperture of 12.8 mm ($n = 16$).

Table 7
ANOVA results on the arcsine-transformed percent alive data from Experiment II

Source of variation	df	SS	MS	F	Pr>F
Protection (absence vs. presence)	1	1017.6	1017.6	2.07	0.1719
Density (clams m^{-2})	3	102.5	34.2	0.25	0.8618
333 vs. mean of rest	1	0.8	0.8	0.01	0.9410
666 vs. (1332 and 2664)/2	1	5.3	5.3	0.04	0.8450
1332 vs. 2664	1	96.4	96.4	0.70	0.4069
Protection×density	3	1224.5	408.2	2.97	0.0425
Absence vs. presence×333 vs. rest	1	1081.1	1081.1	7.87	0.0076
Absence vs. presence×666 vs. 1332, 2664	1	20.3	20.3	0.15	0.7023
Absence vs. presence×1332 vs. 2664	1	123.1	123.1	0.90	0.3493
Box (protection)	14	6870.4	490.7	2.08	0.0246
Netting: absent	7	5355.6	765.1	4.38	0.0007
Netting: present	7	1514.8	216.4	0.97	0.4536
Density×box (protection)	42	5770.9	137.4	0.58	0.9676
Error	64	15,078.2	235.6		
Total	127	30,064.1			

The type I error rate was adjusted to α' =0.0169 for each of the three single-degree-of-freedom orthogonal contrasts (n=2).

3.2.2. Growth

Unlike Experiment I, rg depended whether or not clams were protected from predators. Growth of animals within protected boxes was 4.1% slower ($P<0.05$) than in boxes without netting ($65.1\pm1.19\%$ vs. $69.2\pm1.34\%$, n=63; Table 8). However, this amounted to a difference of only 1 mm in final mean SL between protected (24.3 ± 0.18 mm) and unprotected (25.3 ± 0.21 mm) treatments. Effects of increasing clam density on growth also were significant ($P<0.05$). The trend analysis (Table 8) demonstrated the response to be cubic in nature, suggesting a depression in growth especially at the highest density (Fig. 7). Mean difference between the fastest (333 m^{-2}=$69.7\pm2.35\%$, n=30) and slowest

Table 8
ANOVA results on relative growth data from Experiment II

Source of variation	df	SS	MS	F	Pr>F
Protection (absence vs. presence)	1	0.064	0.064	5.64	0.0323
Density	3	0.064	0.022	3.21	0.0325
Linear	1	0.021	0.021	3.15	0.0832
Quadratic	1	0.001	0.001	0.16	0.6942
Cubic	1	0.042	0.042	6.45	0.0149
Protection×density	3	0.042	0.014	2.07	0.1186
Box (protection)	14	0.159	0.011	0.98	0.4791
Density×box (protection)	42	0.282	0.007	0.58	0.9684
Error	62	0.718	0.012		
Total	125	1.329			

Data were not transformed. No live clams were found in two of 128 pots on 6 October 1991 resulting in unbalanced data. Type III sums of squares were used in all hypothesis tests. The type I error rate was adjusted to α' = 0.0169 for each of the three single-degree-of freedom contrasts associated with the trend analysis (n = 2).
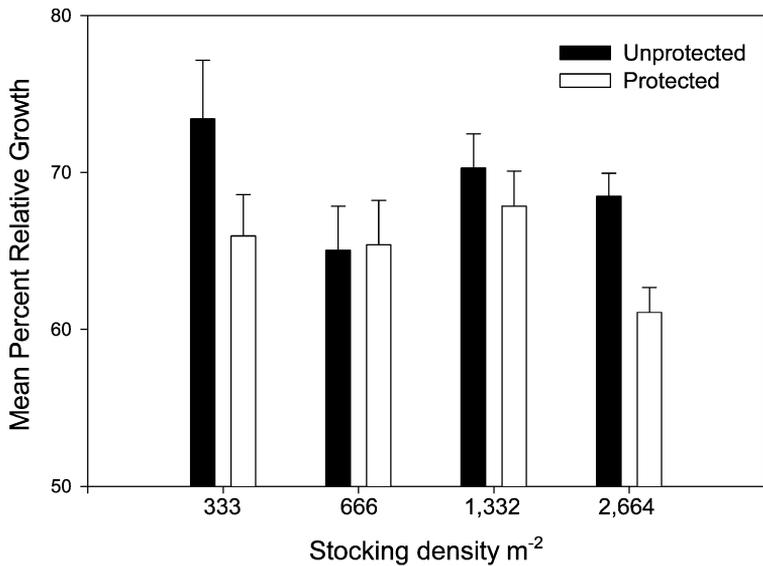
Fig. 7. Mean relative growth +95% confidence interval for hatchery-reared clams (14.6±0.182 mm, $n=100$) planted at each of four stocking densities in experimental units (Area = 0.0187 m^2) within protected (12.8 mm extruded plastic netting; see Table 1; $n=8$) and unprotected 1-m^2 boxes ($n=8$) at Duck Brook Flat, Cutler, ME, USA (Experiment II: 15 April to 6 October, 1991). ANOVA revealed a significant ($P<0.05$) density effect on growth and a trend analysis indicated that a negative, cubic relationship between growth and stocking density best described the pattern. Each bar represents mean relative growth of all live individuals within the $n=16$ experimental units of a particular density treatment.

growing group (2664 m^{-2}=64.8±1.25%, $n=32$) was 4.9%, which related to less than a millimeter SL difference between these two groups (25.1±0.22 vs. 24.4±0.20 mm; Table 9).

Table 9
Minimum, maximum and mean final SL in millimeters (±1 SE) for hatchery-reared soft-shell clams in Experiment II (Duck Brook Flat near Cutler, ME)

Number m^{-2}	Protection	n	Minimum	Maximum	Mean	Standard error
333	Unprotected	15	21.5	29.3	25.3	0.618
666	Unprotected	16	22.4	29.2	25.2	0.417
1332	Unprotected	16	22.9	27.3	25.6	0.325
2664	Unprotected	16	23.7	27.7	24.9	0.272
333	Netting	15	20.2	26.9	24.5	0.506
666	Netting	16	22.0	27.5	24.4	0.411
1332	Netting	16	22.3	26.2	24.5	0.241
2664	Netting	16	22.2	25.1	23.8	0.206

Study was conducted from 15 April to 6 October 1991, or the period when >90% of the annual shell growth occurs in juveniles of *Mya* (Beal, 1994). Initial mean SL of clams was 14.6±0.18 mm. Netting was 12.8 mm Extruded (n = number of experimental units containing live clams).

3.2.3. Benthic sampling and wild spat

One soft-shell clam (4.2 mm SL) was found within the 20 benthic cores on 15 April 1991 (2.8 ± 2.8 m^{-2}) and only six clams were sampled from cores taken on 6 October (16.7 ± 11.5 m^{-2}). Mean SL of these clams was 12.6 ± 4.04 mm (three were >20 mm while the rest were recent settlers [i.e., <5 mm]). Total number of spat sampled from the 128 experimental units was 17 (mean SL=3.1 ± 0.34 mm); 10 spat were found in unprotected units. No significant effects of clam density or type of protection were detected on numbers of spat.

4. Discussion

4.1. Effects of predation and clam density on survival and growth of cultured Mya

Many field studies have demonstrated an enhancement in survival of juvenile cultured bivalves by deterring predators with plastic netting (Spencer et al., 1992; Smith and Langdon, 1998; Fernandez et al., 1999; Cigarria and Fernandez, 2000). Here, we found that protecting clams <12 mm SL with netting (Experiment I) increased their survival by an average of 13%, but we did not find comparable enhancement for clams planted at initial sizes of ca. 15 mm SL (Experiment II). Although there was no significant clam size×type of protection interaction in Experiment I (Table 3), netting resulted in a 9.4% and 16.7% increase in survival among large (11.8 mm SL) and small (8.5 mm SL) clams, respectively. Clam survival at SC was size dependent (sensu Juanes, 1992). After a year, we found, on average, ca. 8% more live animals in experimental units initially stocked with large vs. small clams. Similar size-dependent survival has been found in field trials with hard clams (Hurley and Walker, 1993), Manila clams (Cigarria and Fernandez, 2000), cockles (Mascaro and Seed, 2000), and the deeper burrowing *Yoldia notabilis* (Yokoyama) (Nakaoka, 1996).

Crushing and drilling predators gained entry to some protected boxes at both sites (Tables 2 and 6), yet none of the nets covering the boxes had been ripped or torn. Scouring and some apparent digging did occur around several boxes at SC, but not at DBF. Mean percent survival in many of the protected boxes at SC was >95%, suggesting that predators had been successfully excluded. However, as Fig. 2 demonstrates, predators were capable of removing nearly all animals from several protected boxes. Although no green crabs (*Carcinus maenas* [L.]) were recovered from any of the boxes at SC, numerous 35–50 cm spotted wrymouth eels, (*Cryptacanthodes maculatus* Storer) were found throughout the matrix area in June 1991 including the boxes. These benthic fish construct intricate branching burrows 3–6 cm wide to depths >0.75 m (B. Beal, personal observation) and have been observed to contain soft-shell clams in their stomachs at times (Bigelow and Schroeder, 1953). Evidence of their predatory activities was seen at the entrance to their burrows, which was littered typically with crushed shells of blue mussels (*Mytilus edulis* L.), periwinkles (*Littorina littorea* [L.]), and Baltic clams (*Macoma balthica* [L.]). Ten fish found inside the boxes in June 1991 were taken to the laboratory and their stomachs and intestines dissected; however, only the sand shrimp, *Crangon septemspinosa* Say was readily distinguishable.

Neither type of netting (flexible vs. extruded) nor aperture size made a difference in terms of growth or survival responses of small *Mya* (Experiment I; Table 4). There was no difference in growth between protected and unprotected treatments at SC, but we did observe a significant reduction in growth (4.1%) at DBF (Table 8). Other investigators have found similar reductions in bivalve growth between fully protected and unprotected experimental units and have attributed this growth depression to the presence of predators (Peterson and Black, 1993; Nakaoka, 2000). Beal et al. (2001) examined growth of cultured individuals of *M. arenaria* (12.4 mm SL) along a tidal gradient at a field site within 2 km of SC during 1996 (latitude 44°36′ 48″N, 67°33′ 43″W). Growth of clams at the low tide mark held in fully protected units (similar to this study), which predators (*C. maenas* and *Euspira heros* Say) somehow gained entrance to, was significantly less (6.6%) than growth of animals in unprotected units. Although we discovered signs of predator foraging within protected units at DBF (Table 6), the exact mechanism(s) for growth reduction in protected vs. unprotected boxes is unknown.

We decided to use boxes to lift mesh above the level of the mud flat because in previous trials where nets were applied directly to the mud flat surface, survival of small clams was poor (<25%; Beal, 1994). The physical gap between the clams and the mesh covering did not result in increased sedimentation or apparently interfere with clam feeding as survival within protected boxes over a 1-year period was relatively high (>70%) and independent of netting type. Other studies have shown similar results. Smith et al. (1955) used 25 mm chicken wire mesh to protect >16 mm *Mya* from green crabs and horseshoe crabs (*Limulus polyphemus* L.) in Massachusetts. When wire was raised on boards off the sediment surface 2.5 cm, clam survival increased slightly compared to those protected by the wire in contact with the mudflat. More recently, Spencer et al. (1992) investigated the effective- ness of five types of plastic netting on survival of Manila clams, *T. philippinarum*, in boxes on intertidal beaches near Conwy in Wales, UK. When lightweight, flexible netting (6 mm aperture) was placed flush with the sediment surface, survival (% recovered) of 10–12 mm clams after 2 weeks ranged from 2% to 36%. Provision of a 5 cm gap between clams and netting resulted in a 93% survival over the same period. Unlike the present study, however, Spencer et al. (1992) found that net rigidity was an important factor in protecting newly planted clams against green crab attack. Survival increased with increasing rigidity of the net. Walker and Heffernan (1990) tested the effect of varying mesh size on survival of *M. mercenaria* (19.5 mm SL) and surf clams, *Spisula solidissima* (Dillwyn) (41.5 mm SL), in cages protected with rigid netting (aperture sizes between 3 and 19 mm) near Skidaway Island, GA, USA. Although their cages were designed to include a 5 cm gap between the sediment surface and netting, hard clams were washed out of cages with the largest mesh while in some areas siltation was so severe that cages filled too quickly to benefit from the netting. The investigators concluded as long as initial size of bivalve seed was greater than mesh aperture, netting size had no effect on clam survival. We observed no differential loss of clams from protected boxes at SC according to initial size, although it would have been possible for clams 8.5 mm SL to have been washed from boxes with the largest aperture.

Seven of the eight boxes at DBF showed signs that predators had gained access to protected boxes as evidenced from chipped and drilled valves; however, we observed no density-dependent foraging. Local increases in intraspecific density of marine benthic in-

vertebrates have been shown to influence negatively several life history parameters including growth and/or gonadal mass (Peterson, 1982a; Ólafsson, 1986; Peterson and Black, 1987; Jensen, 1992;), migration rate (Peterson and Andre, 1980; Peterson et al., 1982; Ambrose, 1986; Wilson, 1989; Commito et al., 1995), survival (Lipcius and Hines, 1986; Mansour and Lipcius, 1991; Hines et al., 1997), and recruitment (Thrush et al., 1997, 2000; but see Peterson and Black, 1993; David et al., 1997). No significant effects of density ($133–2664$ m^{-2}) on clam recruitment were observed in either protected or unprotected boxes at DBF in Experiment II, but relative growth decreased according to a negative cubic function with increasing clam density. Although the actual differences in mean SL of clams between the lowest and highest density treatment was relatively small, the fact that juveniles of *Mya* are capable of exploitative competition for food at these densities is important to clam farmers. Also, since *Mya* increases its pumping capacity/feeding rate with size (Zaklan and Ydenberg, 1997), our results suggest that growth depression may occur at lower densities for larger clams. The growth depression we observed may have been an artifact of our experimental design since boxes potentially interrupted near-bottom lateral currents.

4.2. Clam recruitment

Commercial landings of soft-shell clams have declined dramatically in Maine during the past 15 years (NMFS, 2001). One hypothesis is that this is a recruitment-limited system (sensu Peterson et al., 1996) and there are insufficient quantities of wild spat settling onto mud flats to overwhelm natural predation and other biotic or abiotic events (Beal and Fegley, 1996). Enhanced numbers of spat were found inside boxes protected with netting at SC, but not at DBF. Although highly variable and dependent on netting treatment, spat density was not influenced by initial clam size (Table 5, Fig. 6). Spat were more likely to occur in boxes protected with netting having an aperture >4.2 mm perhaps because nets with smaller openings tended to foul more severely than other nets.

Clam recruitment is a three-stage process that involves transport to an area followed by settlement (metamorphosis) and subsequent post-larval survival. Assuming equal numbers of larvae were transported to the relatively small matrix area at SC, differences in final spat density among the protected treatments must be due to differential settlement or post settlement mortality. Predators gained entrance to many of the protected boxes in Experiment I where they consumed more small clams than large ones (Tables 2 and 3). Because this rate was independent of netting treatment (i.e., no significant clam size×type of protection interaction), it is presumed that predation on spat that settled into experimental units within the boxes also was uniform across mesh type. This suggests, then, that settlement processes may differ according to type of netting. If this is true, the likely mechanism may be due to interactive effects of aperture size and rate and type of fouling. Planktonic larvae of benthic invertebrates respond to small-scale fluid flows and turbulence like passive particles (Butman, 1989). Although not quantified, nets with the smallest aperture were fouled heavily with several species of long, slender brown and red seaweeds. The movement of these macroalgae may have negatively influenced clam settlement much the same as algal canopies reduce recruitment of algal zygotes (i.e., preemption, sweeping; reviewed by Vadas et al., 1992).

Deploying plastic netting to areas of the soft-bottom intertidal may be a viable method to enhance locally wild clam abundance. For example, more than three times fewer spat were found in unprotected boxes at SC compared to boxes covered with nets having >6.4 mm apertures. Several Maine communities have begun planting seed clams (10–12 mm SL) near the mid intertidal under 6.4 mm flexible netting (25-m^2 strips raised above the bottom ca. 5 cm) at densities between 300 and 500 m^{-2} (B. Beal, personal observation). On several occasions when these protected areas have been sampled 6 months after seeding (late fall), densities of natural spat >500 m^{-2} have been observed (D. Wallace, Brunswick, ME, personal communication; L. Ranquist, Swans Island, ME, personal communication; B. Beal, personal observation). Samples taken in adjacent, unseeded and unprotected areas contained fewer than 50 wild spat m^{-2} (B. Beal, personal observation).

No enhancement in spat density due to the presence of netting was observed at DBF where recruitment was very low compared to that observed at SC. One explanation may be plankton patchiness. Perhaps few larvae were transported to the study area at a time when they were competent to settle. Another may be due to the time of year when the experiment was terminated. We assume that *Mya* settle during August and into early September in eastern Maine (Stickney, 1964; Beal, 1994). If spawning occurred later in the year during 1991, terminating the experiment early in October may have missed the pulse of settlers. A third hypothesis is that settlement may have occurred shortly before the experiment was terminated, but because samples were washed through a 0.5 mm sieve, the recently metamorphosed animals may not have been retained efficiently. Finally, it is possible that recruitment at DBF is year-specific and that our experiment was conducted during a year when clam settlement was generally poor.

4.3. A mariculture strategy for soft-shell clams in Maine and the northeast US

Today, soft-shell clam culture is in its infancy in Maine, USA. Since 1987, 45 of 70 coastal communities in that state that have management programs for clams have participated sporadically in a public stock enhancement program through BIRSH. Since 1989, research has been conducted on aspects of hatchery production (Beal et al., 1995) as well as field grow out strategies (Beal, 1994). Although not exhaustive, those investigations, as well as results presented here, provide the first quantitative assessment of various biological and physical factors that influence survival and growth of hatchery-reared seed of *Mya*. This information can be used to make recommendations concerning future grow out programs for communities or private entrepreneurs.

Clam survival is positively size dependent. Therefore, efforts to maximize yields should use the largest size seed available. Because seed costs rise sharply with size (Fig. 1), one must consider how to minimize these costs to attain highest yields. From results presented here and elsewhere (Beal, 1994; Beal et al., 2001), clams ranging in SL between 8 and 10 mm should be planted between the mid and low tide mark in early to mid-April (seawater temperature = 3–4 °C) after large ice floes have melted and the probability of severe storm events is low. An April planting will ensure that >95% of the yearly shell accretion will occur. Waiting until June to plant seed, for example, would mean the loss of an estimated 15–20% of annual shell growth (Beal, 1994). Protecting small clams with netting will

result in an approximate 17% enhancement in survival during the first year to levels of nearly 80%. Based on cost of netting vs. yield (Tables 1 and 2), small clams should be protected with flexible netting (6.4 mm aperture) that is raised somehow above the mudflat surface. In our work with fishing communities, we routinely affix nine circular styrofoam floats [10 cm diameter × 10 cm thickness] to the bottom side of large nets—4.25 × 6.75 m. In sandy sediments, we secure the net perimeter by placing the outermost 25 cm edge into a 15 cm dug furrow and then fill in the furrow with the excavated sediments. In muddy sediments, we walk along the 25 cm periphery of the net to secure it. In both instances, during tidal inundation, the floats permit the netting to rise above the flat surface ca. 5–7 cm. The actual seeded area is 25 m^2.

Because effects of crowding on soft-shell clams >30 mm are unknown at this time, a conservative estimate of stocking density would be 333–666 m^{-2} (Tables 6 and 9; Fig. 7). Under these conditions, clams should attain sizes between 25 and 30 mm SL by late fall. Because *Mya* burrow deeper in the sediments with increasing SL (Zaklan and Ydenberg, 1997), animals that attain these sizes would be found at depths between 5 and 8 cm (Zwarts and Wanink, 1989), which should insulate them from effects of ice during most winters as well as help provide a depth refuge from large burrowing predators (Commito, 1982). Although routinely done by fishing communities but eliminated from the experimental design at SC, netting should be swept clean periodically and then removed by late November or early December to eliminate damage or complete loss due to ice (Ellis and Waterman, 1998). Nets can be reused the following April to protect the next crop of seed clams.

Although a complete financial feasibility analysis for soft-shell clam mariculture is beyond the scope of this work, using only clam seed and netting costs allow a crude estimate of a break-even point. For many commercial hatcheries, one million 8–10 mm SL seed clams would cost a community or entrepreneur between $18,000 and $25,000 (Fig. 1). To protect these seed with 6.4 mm flexible netting (Table 1) with affixed styrofoam floats ($1 each) at stocking densities between 333 and 666 m^{-2}, would be an additional $1411 to $2822. Using the most recent (1999) average wholesale price per bushel (22.73 kg) of $69.00 for Maine clams (DMR, 2001) and a 1400-count for the number of legal size (50.8 mm SL) clams per bushel (B. Beal, unpublished data), a survival rate between 39.4% and 56.5% is required to recover initial costs of seed and netting (Table 10).

Rather than purchasing 8–10 mm SL seed, another less preferred option for mariculturists and fishing communities would be to obtain smaller clams (ca. 3 mm SL) and, using floating nursery trays located in protected coves, grow clams to field plantable sizes (Beal, 1994). This option, however, would add an extra year of handling and growing animals before they should be field planted. For example, at BIRSH, 5000–7500 clams (3 mm) are placed in wooden trays (1.2 × 0.9 × 0.08 m) lined with a 1.8 mm nylon "window screening" in late May through July. Each tray costs ca. $25 to produce. Animals attain field planting sizes of 8–10 mm SL by September or October. Since clams cease accreting shell in late October or early November, they will not reach a size large enough to escape most predation and weather-related events that may occur during the winter months. Instead, these clams are held over the winter (sensu Beal et al., 1995). Once total costs for purchasing 3 mm SL clams from most commercial hatcheries ($8.50 to $11 per thousand; Fig. 1), producing floating trays ($3325 to $5000), overwintering the 8–10 mm SL individuals ($400) and protecting them once they are planted ($1411 to $2822) are calculated, the overhead costs are very

Table 10
Estimates of the range of profits (in US dollars) related to expenses incurred with the purchase and field planting of one million 8–10 mm SL cultured juveniles of *M. arenaria* and their survival rate to commercial size (50.8 mm SL) at two field planting densities (333 and 666 m^{-2})

Percent survival	Wholesale price ($) per bushel	Profit range	Percent survival	Wholesale price ($) per bushel	Profit range
30	50	−8697 to −17,108	60	50	2017 to −6394
	70	−4411 to −12,822		70	10,589 to 2118
	90	−125 to −8536		90	19,160 to 10,749
	110	4160 to −4251		110	27,731 to 19,320
40	50	−5125 to −13,536	70	50	5589 to −2822
	70	589 to −7822		70	15,589 to 7178
	90	6303 to −2108		90	25,589 to 17,178
	110	12,017 to 3606		110	35,589 to 27,178
50	50	−1554 to −9965	80	50	9160 to 749
	70	5589 to −2882		70	20,589 to 12,178
	90	12,732 to 4320		90	32,017 to 23,606
	110	19,874 to 11,463		110	43,446 to 35,035

Purchase price of hatchery-reared seed clams = $18,000 to $25,000 (Fig. 1). Costs to protect clams during their first growing season with 6.4 mm flexible netting (Table 1) buoyed with styrofoam floats are $2822 and $1411 at stocking densities of 333 (120 nets) or 666 (60 nets), respectively. (Labor costs were not included in these cost/benefit estimates.) One bushel = 50 pounds, or 22.73 kg.

similar to costs for purchasing 8–10 mm SL clams directly from a hatchery ($13,636 to $19,222). A third scenario would be to grow small cultured seed (ca. 1–2 mm SL) in a shore-based, floating, or tidal-powered upwelling system (e.g., Rhode et al., 1994; Davis et al., 2000); however, costs to produce plantable seed, as well as maintain and manage an upweller, are more costly than to produce and manage floating trays for the purposes of producing 8–10 mm seed (B. Beal, personal observation).

Results from published accounts of growth and survival of soft-shell clams >30 mm SL in nearby Canada (Newcombe, 1935, 1936) and near Gloucester, MA (Brousseau, 1978, 1979) can be used to help develop initial culture strategies. The goal is to plant areas with the highest density of seed that will ensure good survival and not limit growth in an effort to reduce material cost of nets and floats as well as labor costs related to harvesting. For hard clams in a variety of habitats, stocking densities between 500 and 1100 m^{-2} are considered maximum (Walker, 1984; Malinowski, 1986; Adams et al., 1991) so our recommendation of densities between 333 and 666 m^{-2} for hatchery-reared soft-shell clams is conservative. Survival rates >50% for other cultured bivalve species are considered good (Adams et al., 1991; Spencer et al., 1991). Mean survival rate for 8.5 mm seed protected with 6.4 mm flexible netting at SC was excellent (82.5%, Table 2; Fig. 2) and increasing density to levels >333 m^{-2} had no detrimental effect on this rate among larger seed (Tables 6 & 7). Once animals attain a size of 25–30 mm SL [approximately 1 year in eastern Maine between mid and low tidal areas (Beal et al., 2001)], survival rates to legal size (50.8 mm SL) is >80% (Brousseau, 1978; Commito, 1982). Above densities of 1332 m^{-2}, growth rates of protected clams (14.6 mm SL) appeared somewhat depressed

(Fig. 7), but animals held below 1332 m^{-2} had growth rates that were similar to those reported by Newcombe (1935, 1936) at Clam Cove, New Brunswick, where animals 18–30 mm in length were held in protective boxes at densities of 500 m^{-2}. Therefore, annual growth rates obtained in this study are considered representative of wild clams at much lower densities in eastern Maine that take between 4 and 5 years to reach a commercial size of 50.8 mm (Dow and Wallace, 1961).

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