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BIOTIC AND ABIOTIC FACTORS INFLUENCING GROWTH AND SURVIVAL OF WILD AND CULTURED INDIVIDUALS OF THE SOFTSHELL CLAM (*MYA ARENARIA* L.) IN EASTERN MAINE

BRIAN F. BEAL*
University of Maine at Machias, 9 O'Brien Avenue, Machias, Maine 04654

ABSTRACT A series of intertidal field experiments was conducted from 1986–2003 in eastern Maine to examine biotic and abiotic factors influencing the growth and survival of wild and cultured individuals of the softshell clam, *Mya arenaria* L. Separate experiments examined: (1) the efficacy of transferring sublegal wild clams (<50.8 mm SL) from areas near the high intertidal zone where shell growth was slow to areas where growth was predicted to be faster; (2) effects of tidal height on wild and cultured clam growth; (3) effects of spatial variation on cultured clam growth; (4) dispersion and growth of cultured juveniles in small experimental units; (5) effects of the naticid gastropod, *Euspira heros* Say, predation on survival of wild and cultured clams and (6) the species composition of large, crustacean predators that forage intertidally during periods of tidal inundation. Protective netting (4.2 mm aperture) increased recovery rate of transferred clams by 120% and resulted in a 3-fold enhancement of wild recruits. Effects of tidal height on wild clam growth revealed complex behaviors in >0 y-class individuals. Clams growing near the upper intertidal take >8 y to attain a legal size of 50.8 mm SL, whereas animals near the mid intertidal generally take 4.5–6.5 y. Unexpectedly, clams initially 38–54 mm SL and growing near the extreme low tide mark at a mud flat in Eastport, Maine, added, on average, <2 mm of new shell in a year, which was 8–10 mm SL less than animals at higher shore levels. It is hypothesized that biological disturbance by moon snails, that consumed >90% of clams at the low shore levels, contributed to this slow growth. In another field trial from 1986–1987, moon snails and other consumers were allowed access to clams ranging in size from 15–51 mm. *E. heros* preyed on clams over the entire size range and attacked clams between 31–40 mm at a rate that was nearly double what had been expected. Mean snail size was estimated to range from 10–52 mm shell height (SH), based on a laboratory study that yielded information about the linear relationship between snail size and its borehole diameter. In an experiment from June to September 1993, moon snails consumed >70% of juvenile clams (ca. 10 mm SL) within a month after planting at each of three tidal heights. Snail sizes ranged from 15–20 mm SD with larger individuals occurring near the upper intertidal zone. Green crabs, *Carcinus maenas* (L.) also prey heavily on softshell clam populations, but most studies that use shell damage to assign a predator have assumed that all crushing and chipping predation is because of this invasive species. An intertidal trapping study demonstrated that both green crabs and rock crabs, *Cancer irroratus* Say, are present during periods of tidal inundation, with the latter species accounting for ca. 40% of large crustacean numbers.

KEY WORDS: *Mya arenaria*, softshell clam, Maine, growth, predation, *Euspira heros*, *Carcinus maenas*

INTRODUCTION

In Maine, USA, softshell clams, *Mya arenaria* L., are the third most important commercial marine species harvested behind lobster, *Homarus americanus* Milne Edwards, and cultured salmon, *Salmo salar* L. From 2001–2004, dockside clam landings in Maine averaged (±95% CI) 1113.9 ± 99.7 metric tons (worth $15.9 ± $1.68 million; Fig. 1), worth more than $50 million annually to the state economy (ME DMR 2005).

Each of Maine's 105 coastal communities has the option to manage its intertidal clam stocks within its municipality using one of the oldest comanagement programs in the United States. Beginning in 1962, Maine's State Legislature created a community-based management structure between municipalities and the State of Maine through the Department of Marine Resources (DMR). This structure, or agreement, is called a "shellfish ordinance," and it allows towns to adopt, amend or repeal a set of shellfish conservation measures that regulate the taking of shellfish within the intertidal zone of the municipality. The ordinance is a broadly defined document that includes language about conservation activities, qualifications of a licensee, license fees, limiting effort, harvesting methods and tools, enforcement, the organization and rights of a local stewardship committee and other measures. The first step a town must take once it declares its intention to manage its local clam assets is to adopt a "model ordinance," or general management plan, that outlines basic requirements the state mandates. (Towns not interested in managing their clam stocks are not required to do so, and, therefore, the State must act alone to manage those intertidal flats to the best of its ability.) However, the model ordinance is structured to permit sufficient flexibility to enable a community to benefit from local knowledge, wants and wishes by creating, adopting and regulating its unique management schemes that may exceed the basic provisions set out in the model ordinance. These local modifications are enacted when a community requests them in writing to the DMR, and they are granted by the DMR Commissioner. In this way, two adjacent communities may have a common goal of increasing local clam stocks, but have very different looking shellfish ordinances. There are 3 common requirements of all communities with shellfish ordinances: (1) the management plan be enforced by a warden paid through the town; (2) no clam less than two-inches (50.8 mm) in shell length (SL) can be harvested legally and (3) 10% of licenses sold in a community must be made available to Maine citizens outside the particular municipality. In 2005, 73 communities (or 70%) with intertidal habitat chose to manage those areas for *M. arenaria* production.

Since the inception of the shellfish ordinance, local stewardship committees have adopted a number of shellfish management tools in an attempt to maintain high yields of clams and keep their clamming habitat productive. The following list includes management activities that have been used in Maine since 1962—no community has adopted all of the activities: (1) limiting the number of licenses sold; (2) restricting harvest volumes; (3) limiting all harvesting to recreational diggers; (4) limiting when harvesting can

*Corresponding author: E-mail: bbeal@maine.edu

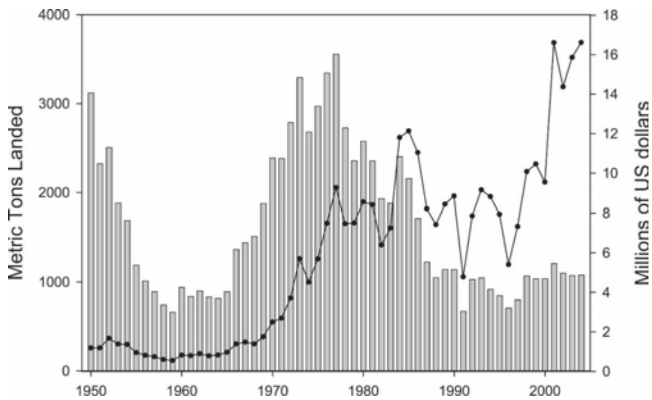

Figure 1. Commercial landings of softshell clams in Maine from 1950 to 2004. Data from: http://www.maine.gov/dmr/commercialfishing/softshellclam.htm.

occur (e.g., no Sunday digging; no night digging); (5) restricting the areas where harvesting can occur (i.e., flat rotations); (6) applying tree brush or snow-fencing to intertidal areas to encourage juvenile clams settlement; (7) applying wire fencing or plastic netting to deter green crab predation and encourage juvenile clam settlement; (8) assessing stock volume and size frequency distributions (i.e., clam surveys); (9) transferring clams from high density/slow growth areas to low density/fast growth areas; (10) enhancing flats with hatchery-reared, or cultured clam seed; (11) installing municipal sewage treatment systems and reducing overboard discharges (e.g., water quality monitoring programs) and (12) municipal leasing of flats (each community has the right to set aside up to 25% of its productive clamming habitat for private clam farming operations).

Shellfish committee members, in concert with State resource managers, must make decisions concerning the status and health of soft-shell clam populations for a variety of applications, the most common being whether the population is abundant enough to be harvested in a sustainable fashion and what level of harvesting will minimize impacts on future populations. Because of logistical constraints imposed by working in marine environments, managers of marine resources often have limited information about important population characteristics such as survival, growth and recruitment rate and how these parameters change spatially and temporally. Rather, decisions about harvest levels, for example, usually are limited to estimates of change in standing stocks and size frequencies through time or between locations.

It is rare that adaptive management strategies and experimental approaches are considered by fisheries managers (but see Botsford et al. 1997, Lenihan & Micheli 2000, Beal & Vencile 2001); however, manipulative field experiments are the strongest and most efficient means available to managers to base decisions about the dynamics of a population (Underwood 1990, Underwood 1991). The field trials reported here are intended to add to a growing literature on soft-shell clam ecology from Maine and western New Brunswick, Canada (Spear & Glude 1957, Welch 1969, Commito 1982a, Commito 1982b, Newell & Hidu 1982, Ambrose et al. 1998, Beal et al. 2001, Beal and Kraus 2002, Whitlow et al. 2003, Auffrey et al. 2004, Logan 2005) and provide information to shellfish stewardship committees and resource managers that increases the scope of their management toolbox.

This contribution summarizes a number of field investigations conducted in eastern Maine since 1986 that focuses specifically on the biotic and abiotic factors affecting growth and survival of wild and cultured softshell clams.

METHODS

Experiment I

Clam Transfers

In 2004, approximately 44% of the 73 Maine communities that actively managed their shellfish stocks participated in some form of transfer program (ME DMR 2005). These activities are very labor intensive because they involve harvesting and transporting wild "seed clams" from areas where growth is slow or retarded (i.e., near the upper intertidal where clam growth can be 95% slower than growth of the similar animals at the low intertidal [Beal et al., 2001]) to areas where growth is faster. Most communities transfer clam seed that is approximately 38–45 mm SL (pers. obs.). To the best of my knowledge, there has been only one attempt to quantify the efficacy of transfers in Maine. Here, information is presented that examines short-term survival, growth and recruitment patterns of transferred clams.

On May 2, 1998, approximately 165 kg of soft-shell "seed" clams were dug by commercial harvesters from the city of Eastport, Maine in the high intertidal zone of a flat near Carlow Island in Passamaquoddy Bay (44°56.34′N; 67°01.77′W). Animals were slow growing, and annual ring counts (Newcombe 1935) indicated that the oldest animals were >15 y old. Clams were sieved, washed, and stored overnight in a walk-in cooler at 4°C. A random sample of these clams ($n = 96$) demonstrated that the ranges of SL's varied from 23.2 mm to 58.5 mm with a mean SL = 39.3 ± 9.5 mm. A relationship between clam mass and clam number was developed for those clams by counting five separate lots of individuals at 0.45, 1.36, 2.27 and 3.18 kg (Count = 0.03 + 107.21 × Mass; $n = 20$; $r^2 = 0.969$; $P < 0.001$). This relationship was used to estimate number of clams seeded into plots (9.3 m^2) at a nearby intertidal flat, Carrying Place Cove, Eastport, Maine (44°54.04′N; 67°01.28′W), at low tide on 3 May 1998. Seeding densities were 0, 4.1, 6.1 and 12.3 kg per plot, or 0, 440, 654 and 1319 clams per plot representing approximately 0, 47, 70 and 142 animals m^{-2}.

Six treatments, with five replicate plots each, were established: (1) 0 kg with a piece of 4.2 mm flexible plastic netting to deter predators; (2) 4.1 kg with netting; (3) 4.1 kg with no netting and surface of flat roughened with clam harvesting hoes (sensu Robinson & Rowell 1990); (4) 6.1 kg with no netting; (5) 6.1 kg with 4.2 mm flexible plastic netting and (6) 12.3 kg with no netting. Treatments were randomly assigned to plots that were established in a 6 × 5 matrix with 5 m between rows and columns. An initial survey of the experimental area failed to locate a single living clam. To estimate the short-term effect of enhancing flats through transferring seed clams, each plot was randomly sampled twice on October 27, 1998 using a coring device (0.02 m^2) to a depth of 20 cm. All transferred clams per core sample were counted and the SL of each live clam was measured to the nearest 0.1 mm using Vernier calipers. It was possible to distinguish "new shell growth" as an obvious white band along the entire ventral margin of the clam.

Several *a priori* contrasts were of interest for both growth and survival variables: (1) Is netting important to retain transferred clams? This was tested by comparing treatments 4 & 5; (2) Does roughening the sediment surface enhance the burrowing rate of clams? This was tested by comparing treatments 2 & 3 and (3) Is there an effect caused by seeding density? This was tested by comparing the mean of treatments 2 & 4 versus 6. In addition, the control plots (without seed) were used to compare recruitment of wild spat (animals <18 mm SL) in netted plots to similar plots containing transferred seed. This was a comparison of the mean of treatment 1 versus the mean of treatments 2 & 5. A conservative decision rule was used for each contrast based on advice from Winer et al. (1991) who cautioned against excessive type I error by reducing α using the following equation:

$$\alpha' = (1 - \alpha)^{1/m}$$

where m = the number of contrasts.

In this instance, because m = 3, α′, equals 0.0170.

RESULTS

Survival

Between 30% and 70% of clams initially transferred were missing from plots at the end of the 5-mo experimental period. Greatest missing rates occurred in the low-density plots. Table 1 demonstrates that protecting clams with netting had no statistically significant effect on clam density after 5 mo ($P = 0.0293$); however, mean density under the netting was approximately twice that in plots without netting (220 ± 35.9 vs. 100.0 ± 36.5 animals m^{-2}; $n = 5$). There was no significant difference in final density between roughened versus nonroughened plots (20.0 ± 14.5 vs. 15 ± 6.0 individuals m^{-2}, respectively). In addition, significant differences in final clam density were observed after 5 mo; however, instead of a 3-fold difference between highest and smallest density treatments that was incorporated into the experimental design (see earlier), a 5-fold difference in final density was observed (95.0 ± 24.0 vs. 17.5 ± 10.3 animals m^{-2}; Table 1; $P = 0.0074$).

Growth

Clam growth was related to initial planting size (Fig. 2), but was unaffected by stocking density, netting and sediment roughening ($P > 0.80$). Clams initially <35 mm added, on average, 8.1 ± 1.14 mm ($n = 13$) of new shell between May and October 1998 compared with 3.4 ± 0.56 mm ($n = 27$) for animals >35 mm ($P = 0.0002$).

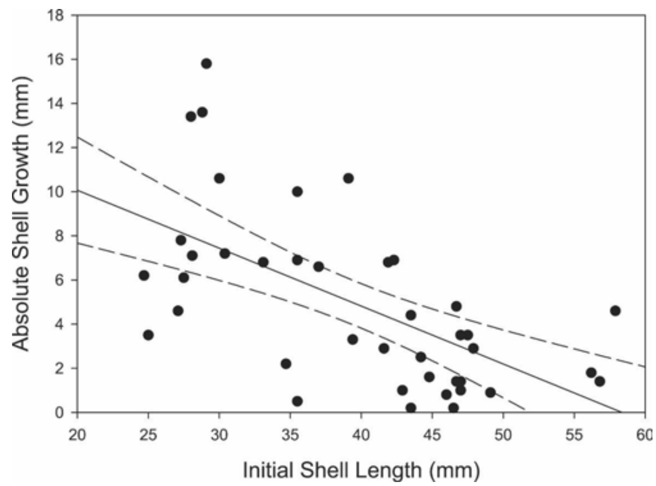

Figure 2. Absolute growth (±95% confidence interval) of softshell clams transferred to Carrying Place Cove in Eastport, Maine from May 2 to October 27, 1998. Y = 15.3–0.262 X; $n = 40$; $r^2 = 0.368$; $P < 0.001$.

Recruitment

No wild spat were found in control plots that did not receive clam seed, nor were spat found in samples from the low density stocking treatment. ANOVA on the square root-transformed number of wild spat (<18 mm SL) per core (Table 2) demonstrated a significant effect because of the presence of the netting as 3.3 times as many spat were found in netted versus unnetted plots (50.0 ± 21.1 versus 15.0 ± 7.6 individuals m^{-2}; $n = 5$). In addition, number of wild spat increased significantly with stocking density ($P = 0.0087$; Table 2) from 15 ± 7.2–45 ± 10.3 individuals m^{-2} ($n = 5$) in plots initially seeded at densities of 70, and 142 animals m^{-2}, respectively. No differences in SL were observed across the seeding treatments for the wild spat ($P = 0.8606$).

Experiment II

Growth of Soft-shell Clams in Eastern Maine

Clam growth rates vary geographically along the coast of Maine. Dow and Wallace (1953) reported that in some areas of eastern Maine, it takes an average of 8 y for *Mya* to reach legal size

TABLE 1.

Analysis of variance on the square root-transformed number of re-seeded clams per 0.02 m^2 sample taken on October 27, 1998 at Carrying Place Cove, Eastport, Maine. Two random samples were taken from each of five replicates of each treatment (2 × 5 × 5 = 50 samples). A priori contrasts appear under the Treatment source of variation and a decision rule equal to α′ = 0.0170 was used.

Source of Variation	df	SS	MS	F	Pr > F
Treatment	4	10.84	2.71	11.87	0.0091
(1) Net versus no net	1	1.54	1.54	8.11	0.0293
(2) Roughened versus not	1	0.01	0.01	0.02	0.8952
(3) Stocking density	2	4.58	2.29	37.84	0.0074
Sample (Treatment)	5	1.14	0.23	0.59	0.7071
Error	40	15.46	0.39		
Total	49	27.44			

TABLE 2.

Analysis of variance on the square root-transformed number of wild clam spat (0-year class individuals <18 mm SL) per 0.02 m^2 sample taken on October 27, 1998 at Carrying Place Cove, Eastport, Maine. Two random samples were taken from each of five replicates of each treatment (2 × 6 × 5 = 60 samples). A priori contrasts appear under the Treatment source of variation and a decision rule equal to α′ = 0.0170 was used.

Source of Variation	df	SS	MS	F	Pr > F
Treatment	5	5.95	1.19	13.81	0.0031
(1) Net versus no net	1	0.90	0.90	10.44	0.0169
(2) Roughened versus not	1	0.00	0.00	0.00	1.0000
(3) Stocking density	2	2.65	1.32	33.91	0.0087
Sample (Treatment)	6	0.52	0.09	0.39	0.8834
Error	48	10.67	0.22		
Total	59	17.14			

(50.8 mm SL). This average decreases in a southwesterly direction where, in the area from Portland to Kittery, it takes approximately 3 y for animals to attain legal size. In addition, tidal inundation may influence growth rates as clams cease growing during periods when the tide leaves the mudflats. To investigate how clam growth is influenced by tidal position, a number of studies have been carried out during the past decade in eastern Maine. Here, results from four investigations are presented that were conducted in Eastport, Jonesport, and Addison.

METHODS

Eastport

Twenty 0.25 m^2 plots (corners marked with wooden stakes) were established at Carrying Place Cove on April 22, 1998 at 10 separate locations ranging from extreme low tide (plots 1–3) to lower mid tide (plots 4–6) to upper mid tide (7–9) to upper tide (plot 10). At each location, replicate plots were established. Wild clams used in the study were dug on April 19, 1998 near Carlow Island (described in the **Clam Transfers** section) and ranged from 23.8–59.0 mm SL. Animals were held in a cold room at 4°C, and on April 21, approximately 170 clams were uniquely marked with an oil-based ink (Mark-Tex Corp.) and measured to the nearest 0.1 mm using Vernier calipers. To facilitate planting the clams and to aid in their burrowing, on April 22 the surface of each plot was roughened using a clam hoe. Then, 17 marked and 10 unmarked clams were pushed into the sediments (so that the posterior margin of each clam was 1 cm below the sediment) in one of the two plots (a) at each location 27 unmarked individuals similarly were planted in the other plot (b). Sediment type varied from location to location along the tidal gradient. Plots became sandier towards the mid-tide area (except for plot 7, which was located in a blue clay sediment). Plots 1–3 typically were exposed only briefly (ca. 30–40 min) on the spring tides of each month, and clam growth rate in these plots was predicted to be the fastest because these animals were able to feed longer each tidal cycle than clams in plots at the higher tidal levels. Conversely, growth rate of clams in plots at the uppermost tidal level was predicted to be the slowest because those plots were exposed daily for the most amount of time during each semidiurnal tidal cycle (ca. 240–300 min).

On April 20, 1999, all 20 plots were excavated and all live and dead animals were taken to the laboratory. Each live clam was examined for a disturbance line believed to coincide with the size of the clam on 22 April 1998 (see an example of this technique for juveniles of *M. arenaria* in Beal et al. 1999). The marked clams enabled me to test the hypothesis that the disturbance line coincided with the size of the animal when it was transferred to the 0.25 m^2 plot. Using calipers, the length of the marked animal at the disturbance line was estimated and recorded. This size is referred to as a "predicted length." After all marked animals from each plot had been measured, these predicted lengths were compared with the actual lengths that had been recorded the previous year. A perfect correlation would result in a line with the equation Y = X. A 2-tailed, one-sample *t*-test was performed to test whether the difference between actual and predicted was zero. Fifty-nine marked individuals (of 170) were found alive in all 10 locations. The mean difference between the actual length and the predicted length for these 59 clams was 0.098 mm (minimum difference was –0.5 mm and the maximum difference was 1.4 mm; Fig. 3). The test revealed that the mean difference was not significantly different from zero (T = 1.836; df = 58; P = 0.072), suggesting that the disturbance line on each valve coincided directly with the handling, planting and other disturbance the animals had endured a year earlier. Because clam growth over the entire year could be discerned, Ford-Walford plots (Walford 1946) were used and then converted to von Bertalanffy equations. These equations were plotted to generate plot- and tide-specific growth rate curves.

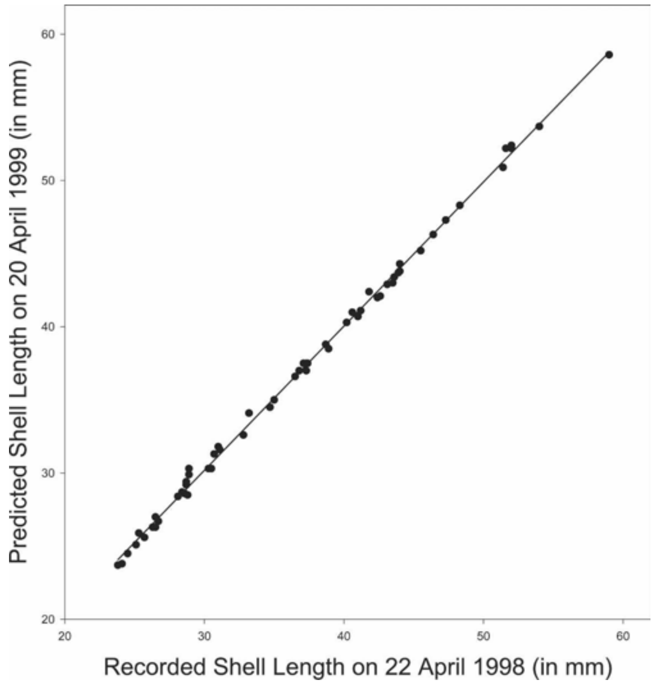

Figure 3. Predicted versus recorded shell length of marked clams from Carrying Place Cove, Eastport, Maine, on April 20, 1999. Predicted SL was based on an obvious disturbance mark in the valve of clams that had been marked with ink near their umbo on April 22, 1998. Because the equation of the line (Y = –0.55 + 1.012 X; *n* = 40; r^2 = 0.998) is not significantly different from Y = X, the disturbance line was used to establish the size of unmarked clams in the growth rate experiment.

Jonesport

Hatchery-reared clams (12.4 mm ± 0.31 mm), produced in 1995 at the Beals Island Regional Shellfish Hatchery (BIRSH; Perio Point, Beals, Maine) and overwintered according to Beal et al. (1994), were placed into plastic horticultural plant pots (15 cm diameter × 15 cm deep) that had been filled with ambient sediments at an intertidal flat (Flake Point Bar, 44°36.75′N; 67°33.72′W) near Jonesport, Maine on 6 April 1996. Experimental units were distributed in three locations along a shore level gradient (low, mid and high intertidal) and stocked at one of three intraspecific densities (330, 660 and 1320 m^{-2}). One-half of all units were covered with a piece of flexible, plastic netting (6.4 mm aperture) to deter predators (Beal et al. 2001). Ten replicates of each of the six treatments were used at each tidal height. To assess clam growth rate, units were collected on December 13, 1996, approximately one month after shell growth ceases in this region (Beal 1994) and two linear measurements (initial and final SL) were taken on all live clams using Vernier calipers to the nearest 0.1 mm. It was possible to discern the initial size of each hatchery-reared clam even though none was marked uniquely because each animal lays down a unique disturbance check in both of its valves at the time it is placed in the sediments (Beal et al. 1999).

In another study at Flake Point Bar, wild clams (size range = 21.4–79.5 mm) were collected from the upper (n = 17) and mid (n = 23) intertidal on November 11, 2004, and the animals aged using annual rings (Newcombe 1935) to estimate tide-specific age-length data. Ford-Walford plots were used to generate von Bertalanffy growth curves.

Addison

On May 10, 2001, hatchery-reared clams (12.4 ± 1.4 mm SL; stocking density = 535 individuals m^{-2}) were added to 24 plastic horticultural pots (as described earlier) that contained ambient sediments at 4 intertidal sites chosen by Addison's shellfish committee (Batson's Beach: 44°31.65′N; 67°41.98′W, Eastern Harbor: 44°30.93′N; 67°43.37′W, Three Brooks: 44°33.56′N; 67°44.81′W, Upper Pleasant River: 44°35.82′N; 67°44.58′W). At each site, experimental units were arrayed in six blocks of four units each (2 × 2 matrix per block with 1-m spacing between rows and columns). To deter predators, in each block, a thin, flexible piece of plastic mesh netting (aperture = 6.4 mm) was affixed to the top of two units using rubber bands, whereas the other two received no netting. Blocks were spaced about 2 m apart and placed between the mid to low intertidal at each site. All units were removed from three of the sites on November 16, 2001, whereas the units were removed from Three Brooks on November 21, 2001. Growth rates for each living clam was determined as described earlier.

ANOVA was conducted on the untransformed mean final SL using the following linear model:

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

where

μ = theoretical mean;

A_i = site (i = 4 sites, factor is fixed);

B_j = Netting Treatment (j = 2, protected versus unprotected, factor is fixed);

C_k = Block (k = 6 blocks per site; factor is random); and,

e_l = experimental error.

RESULTS

Eastport

Most (93%) of the clams in the lower plots were recovered dead with a countersunk hole, typical of predation by the moon snail, *Euspira heros* Say. Only 1 of 68 marked clams was found alive in plots 1a-4a (lowest tidal heights). That animal grew 1.5 mm over the year from 49.6–51.1 mm. Similarly, in a plot with unmarked animals (3b), one live clam (of 27 planted) was found, and it had grown only 4 mm from 38.0–42.0 mm. Plot 4b contained only 3 live, unmarked clams (one had grown 1.9 mm from 54.1 mm to 56.0 mm, the second grew 0.5 mm from 49.1 mm to 50.6 mm, and the third grew 0.8 mm from 48.5 mm to 49.3 mm).

Clam survival in lower mid to upper intertidal plots at Carrying Place Cove (5–10) varied from 50% to 81%, which yielded sufficient data to estimate annual growth rates (Fig. 4). The time to reach a legal size of 50.8 mm SL varied directly with tidal height and sediment type. The growth curves of clams from plots near the lower mid tide (Plots 5 & 6) demonstrate that it would take between 4.5–5.5 y to reach 50.8 mm. Clams in clay sediments within

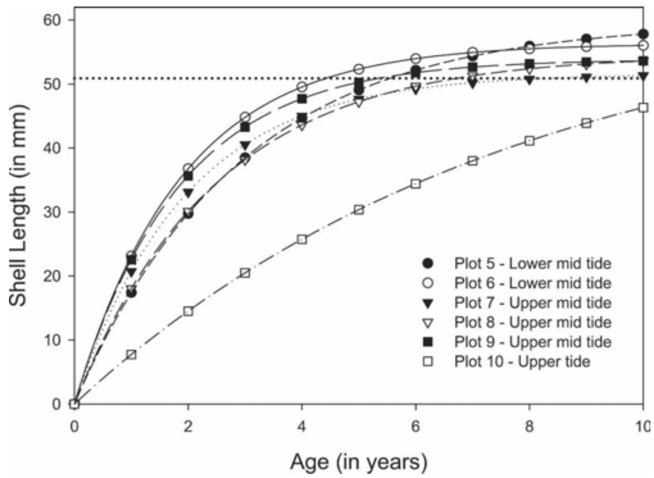

Figure 4. von Bertalanffy growth curves of wild clams along a tidal gradient at Carrying Place Cove, Eastport, Maine from April 22, 1998 to April 20, 1999. The dotted line parallel to the x-axis is the minimum legal size of softshell clams in Maine (50.8 mm, or 2-inches SL).

Plots 7a, b, near the upper mid tide, take 7–8 y to reach legal size; however, animals in adjacent plots at the same tidal height but in more sandy sediments (Plots 8a, b) reach this size in 6.5 y. Growth rate of clams at or near the highest tidal mark are extremely slow (Fig. 4), and animals there may never attain legal size (pers. obs.).

Jonesport

No effect caused by predator exclusion (P = 0.0696) or stocking density (P = 0.0890) on clam growth was detected from April to December 1996; however, tidal height effects were highly significant (P < 0.0001). Final mean SL of animals at the lowest intertidal was 35% greater than those at the mid tide level and 95% greater than those at the upper intertidal. In addition, growth variation decreased significantly from the lowest to highest tidemark (Fig. 5).

From the November 2004 sampling, clam growth was faster at the mid intertidal versus the upper intertidal reflecting differences in tidal inundation (Fig. 6). Clams attain a size of 50.8 mm in 5.8 y at the mid-tide level and 7.8 y near the upper intertidal.

Addison

No differences in growth were observed between clams protected with netting and those that remained unprotected at any of the four sites for the 198-day experiment. Growth rate was fastest at Eastern Harbor where clams increased in SL by an average of 27.0 mm (final mean SL = 39.4 ± 1.2 mm) and slowest at Upper Pleasant River where final mean SL was 31.2 ± 3.5 mm. A small percentage of clams (1.9% and 1.0%) attained at least 50.8 mm SL at Eastern Harbor and Three Brooks, respectively (Fig. 7). ANOVA indicated that site was the only significant source of variation (Table 3) and an *a posteriori* Student-Newman-Keuls (SNK) test demonstrated that clams at Eastern Harbor and Three Brooks attained significantly greater final mean SL's than clams at the other two sites (P = 0.0001).

Experiment III a and b

Dispersion and Growth of Hatchery-reared Juveniles of the Softshell Clam

Many of the small-scale field experiments conducted since 1989 (Beal 1994, Beal et al. 2001; Beal & Kraus 2002) have used

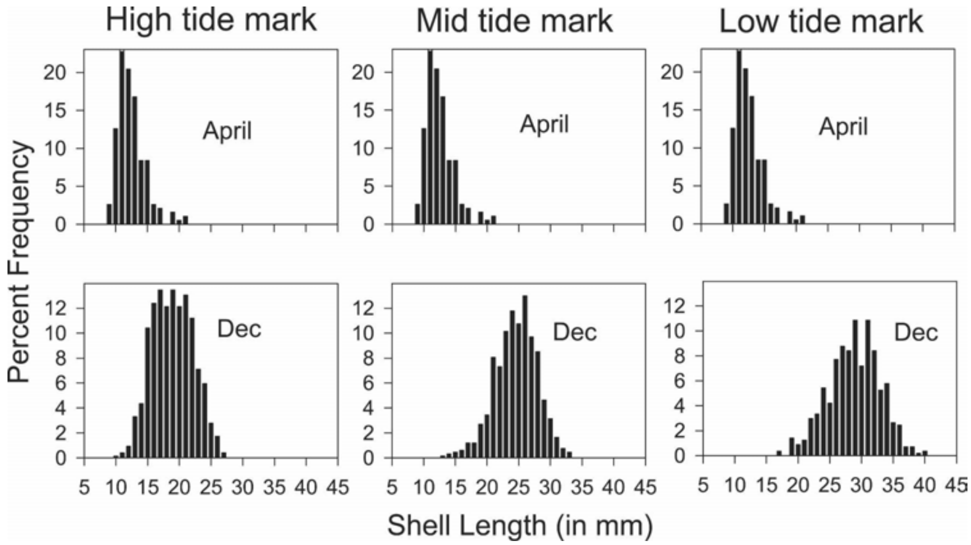

Figure 5. Size-frequency distributions of hatchery-reared clams planted at three different tidal heights at an intertidal flat near Jonesport, Maine from April 6 to December 13 1996. Mean initial SL = 12.4 mm. Most shell growth occurred between early June and August 6, but rates depended on tidal height (high, mid, and low tide plots = 55%, 42.2% and 45.2%, respectively). n_{April} = 191 for all tidal heights; n_{December} for high tide, mid tide and low tide clams = 758, 670 and 571, respectively.

plastic, horticultural plant pots (15.2 cm diameter × 15.2 cm deep with a cross sectional area of 0.0182 m^2). These experimental units are filled with ambient, unsieved sediments, and then buried to their rims in the sediments of a particular intertidal mud flat. Clam juveniles are then pushed gently to a depth of 12–15 mm under the sediment surface within the experimental units. These units are relatively easy to manipulate and establish various treatments within (e.g., stocking density, initial clam size, etc.). To discourage clams from emigrating from these units, a strip of flexible, plastic netting (4.2 mm aperture and measuring 10 cm × 50 cm) typically is affixed to the outside circumference of each pot creating an open enclosure (sensu Beal et al. 2001). The netting, which extends 4–5 cm above the lip margin, purportedly acts as a fence to further decrease the probability of animals somehow escaping by themselves. Strips of the netting do not cover the top of the experimental unit and, therefore, allow predator access to the clams within the experimental units. Often, results of short-term field experiments reveal that missing rates from these open enclosures can be as high as 30% to 40% (Beal et al. 2001). Because the strip of netting is supposed to act as a barrier to emigration, it has been assumed that the missing clams are dead, the result of one or more predation events that directly or indirectly (tidal currents, wind, etc.) remove animals or their shells from the experimental units. In addition, it has been assumed that the strips of netting do not modify local currents and result either in a reduction or enhancement of shell growth.

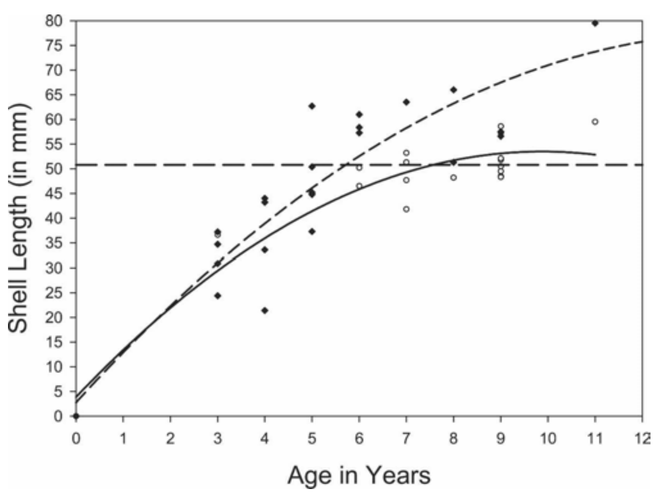

Figure 6. Age-length curves for wild clams collected on November 11, 2004 from two tidal heights at an intertidal flat near Jonesport, Maine. The dashed curve (diamond symbols) represents growth of clams near the mid intertidal (*n* = 17) whereas the solid curve (open circles) represents growth of clams near the upper intertidal (*n* = 22). The dashed line parallel to the x-axis is 50.8 mm, or minimum legal size (2-inches SL).

METHODS

Experiment III a

To test the assumption that the flexible netting strips affixed to the experimental horticultural pot enclosures provide a barrier to migration, a laboratory and field test was designed. In the laboratory at BIRSH, 10 experimental units containing muddy sediments obtained from a nearby mudflat were established (as described earlier). On April 5, 1989, twelve hatchery-reared clams (4–6 mm SL) were added to each enclosure, and then the experimental units were placed in an array on the bottom of a 2,600-L fiberglass tank filled with ambient, unfiltered seawater (4°C). After one hour, during which time all clams had burrowed completely into the sediments, seawater was permitted to flow into the tank at a rate of ca. 5 l min^{-1}. After seven days at this flow rate, sediments in each experimental unit were washed through a 0.5-mm sieve, and all living and dead clams enumerated.

Emigration may depend on flow rate, varying submergence times, changes in temperature between immersion and emersion and other variables that are not controlled in a field setting. It is possible that experimental units with strips of mesh netting surrounding the periphery will act like a predator inclusion cage,

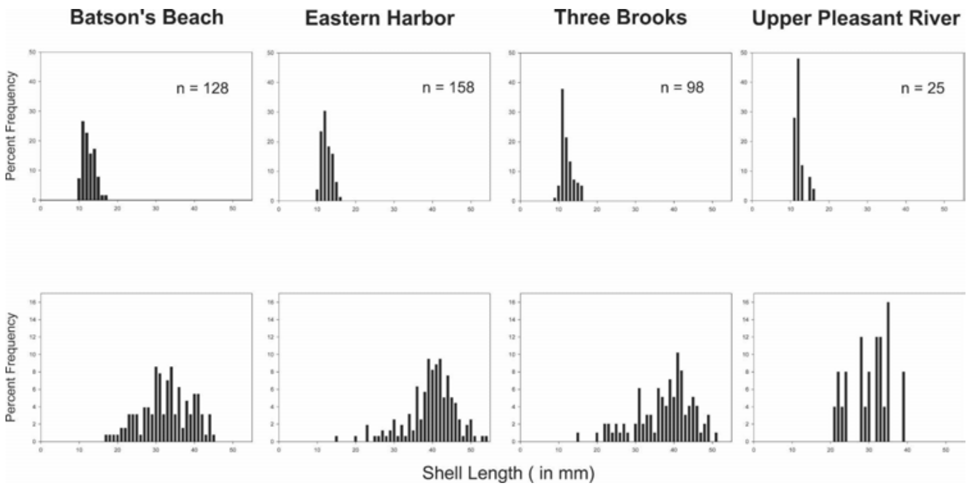

Figure 7. Size-frequency distribution of hatchery-reared softshell clams planted between the mid and low tide mark at four intertidal flats near Addison, Maine (May 10 to November 21 2001). Fastest growth occurred at Eastern Harbor and Three Brooks, where final mean SL ± 95% CI = 38.9 ± 0.98 mm (*n* = 38) was significantly different (*P* < 0.05) from the final mean SL at the other two sites (32.8 ± 1.41 mm; *n* = 31).

enhancing predation by crabs and other consumers. Conversely, the flexible netting strip may deter predators and keep predation rates artificially low. Because laboratory studies cannot adequately reflect field conditions, the potentially confounding effects of emigration from experimental units also were evaluated in the field near the mid intertidal at a mudflat in the town of Cutler, Maine (44°41.22′N; 67°18.59′W). On May 22, 2003, cultured clams (mean SL = 11.7 ± 0.25 mm) were added to experimental units (plastic horticultural pots) with and without a strip of flexible netting (as described earlier) at two stocking densities (12 or 24 clams representing 660 and 1320 m^{-2}, respectively). One half of all units were surrounded by an open ring of solid plastic (11.5 cm wide × 29.0 cm diameter) that was pushed into the sediments 65 mm so that the experimental unit was in the middle of the open ring. The ring was used to help further contain clams that might emigrate from experimental units. The experiment was established as a completely randomized design with 10 replicates for each of eight fully factorial treatments (stocking density, a = 2 levels; netting strip, b = 2 levels; plastic ring, c = 2 levels). Enclosures were added to a 10 × 8 matrix, with 1-m spacing between rows and columns. Both short- and longer-term treatment effects were studied by randomly removing five replicates from each treatment from the matrix after 8 days, on May 30, 2003 and the remaining five replicates after 100 days, on August 30, 2003. Sediments from each experimental unit were washed through a 2-mm mesh. In addition, for units surrounded by a plastic ring, sediments within the area of the ring minus the area occupied by the experimental unit (i.e., 0.066 m^{-2}–0.018 m^{-2} = 0.048 m^2) were sampled to a depth of 14 cm. Each of these samples was processed as described earlier. The relative growth of clams in units with and without strips of flexible plastic netting was assessed in the longer-term study. Relative growth = ([Final SL − Initial SL]/Initial SL) × 100%. A relative growth value of 100% indicates a doubling in SL.

TABLE 3.

Analysis of variance on the untransformed mean final SL of hatchery-reared individuals of *M. arenaria* from 10 May to 21 November 2001 at four lower mid-intertidal sites in Addison, Maine. Ten clams (12.4 ± 1.4 mm SL) were added to protected (netting = flexible, 6.4 mm aperture) and unprotected experimental units (A = 0.0182 m^2) filled with ambient sediments and arrayed in six blocks per location. (n = 2 or 1 depending on survival.)

Source of Variation	df	SS	MS	F	Pr > F
Site	3	525.13	175.04	12.57	0.0001
Protective netting	1	13.27	13.27	1.41	0.2541
Site × Netting	3	31.44	10.48	1.11	0.3756
Block (Site)	18	250.63	13.93	1.66	0.1120
Netting × Block (Site)	15	141.52	9.43	1.12	0.3820
Error	28	235.28	8.40		
Total	68	1197.27			

Experiment III b

Another assumption is that the strips of netting used to enclose juvenile clams within experimental units (A = 0.0182 m^2) do not affect their growth. On May 22, 2003, a generalized completely randomized block design (sensu Underwood 1997) was established at the mid intertidal of the mudflat in Cutler, Maine (see earlier). Eighty experimental units were filled with ambient sediments and pushed into the mud in blocks of four units each. Ten blocks contained units with strips of netting surrounding its periphery and extending above the sediment surface 4–5 cm (as described earlier). The remaining 10 blocks contained units without any strips of netting. Twelve hatchery-reared individuals (660 m^{-2}) were added to two of the units within each block, whereas the other two received 24 clams (1320 m^{-2}). Mean initial SL was 12.9 ± 0.4 mm (n = 100). On 29 August 2003, the contents of each experimental unit were sieved using a 2-mm mesh and the initial and final SL of each live clam measured to the nearest 0.1 mm using Vernier calipers. ANOVA was conducted on the untransformed mean relative growth using a linear model similar to that described (see **Experiment II: Addison**) earlier except:

A_i = Rim netting (i = 2, with and without; factor is fixed);

B_j = Intraspecific clam density (j = 2, 660 versus 1320 m^{-2}; factor is fixed); and,

C_k = Block (k = 10 blocks per rimming treatment; factor is random).

RESULTS

Experiment III a

All 120 clams were recovered alive from the experimental units within the tank at BIRSH, and none had escaped the enclosures.

In the short-term field trial, a small proportion of juvenile clams were missing (mean missing rate = 4.5 ± 1.9%; n = 40). Missing rate was unaffected by stocking density (F = 1.17; df = 1, 32; P = 0.4187) or the presence of the strip of flexible plastic netting affixed to the outside circumference of each enclosure (F = 0.13; df = 1, 32; P = 0.5625). Of those experimental units rimmed with netting and further surrounded by a plastic ring, only one live clam of the 180 transplanted to those units (24 × 5 reps + 12 × 5 reps), or <1%, had migrated from the unit (i.e., was found within the sediments outside the unit but within the area delineated by the plastic ring). For units without plastic strips of netting five clams were found in areas delineated by the ring. Two were alive (1.1%) and 3 were dead (2 with undamaged valves and 1 with crushed valves).

In the 100-day field experiment, the rate of missing clams pooled across all treatments was 24.7 ± 3.2% (n = 40); however, as in the case for the short-term trial, missing rate was unaffected by the presence of the strip of flexible netting ($\bar{x}_{\text{no netting}}$ = 27.1 ± 5.1% versus $\bar{x}_{\text{netting}}$ = 22.3 ± 3.8%, n = 20; F = 0.23; df = 1, 32; P = 0.6338). The addition of a ring of plastic around experimental units helped determine the fate of missing clams. Only one live clam was sampled outside an experimental unit and within the area surrounded by the plastic ring (from an experimental unit without a strip of netting and stocked initially with 24 clams), whereas 40 clams were found dead, with crushed or chipped valves (typical of crustacean predation) in the same area. By adding the ring of plastic surrounding experimental units, the rate of missing clams dropped from 36.0 ± 3.4% (units without rings, n = 20) to 13.3 ± 3.9% (units with rings, n = 20) (F = 29.09; df = 1, 32; P < 0.0001). Stocking density did not influence rate of missing clams (F = 3.92; df = 1, 32; P = 0.0565).

Clams grew similarly in units with and without strips of netting (P = 0.9948). Mean relative growth in experimental units with strips of netting was 99.1 ± 1.9% (n = 40) whereas growth in units not surrounded by the rim of netting was 99.7 ± 2.7% (n = 38). In addition, no density effects on growth were detected (P = 0.8174).

Experiment III b

No significant difference in relative clam growth was found between experimental units with (99.1 ± 3.83%, n = 40) versus without the rim of netting (99.7 ± 5.56%, n = 38) used to enclose clams (P = 0.9948; Table 4). Mean final SL of clams in units with netting strips was 25.3 ± 0.51 mm versus 25.4 ± 0.57 mm for clams in units without the strips. In addition, stocking density had no effect on relative clam growth.

Experiments IV–VI

Predation Studies

Predation is the single most important and significant factor affecting survival of juvenile clams in eastern Maine (Commito 1982b, Beal 1994, Beal et al., 2001, Beal and Kraus 2002, Beal in press). Efforts to deter predators using plastic netting have been used recently; however, when the exotic European green crab, *Carcinus maenas* (L.), became a nuisance and major threat to clam populations in Maine during the 1950s, chicken wire (spread out over the flats and established as 0.5–0.75 m tall fences with a flange on top) was used to slow down and reduce the effectiveness of this crustacean predator within the intertidal zone (D. Wallace, Brunswick, ME, pers. comm.). Green crabs have been implicated as the cause of the sudden decline of the Maine softshell clam fishery during the 1950s (Glude 1955, Grosholz & Ruiz 1996; Fig. 1). Another major predator of *M. arenaria* in eastern Maine is the moon snail, *Euspira heros*. According to Commito (1982b), this naticid gastropod preys on *Mya* until clams reach 30 mm SL, then mortality caused by *E. heros* is much reduced.

Here, results are presented from three field studies in eastern Maine to assess the importance of moon snail and green crab predation on wild and cultured individuals of the softshell clam.

TABLE 4.

Analysis of variance on the untransformed mean relative growth of hatchery-reared juveniles (mean initial SL = 12.9 ± 0.4 mm) of the softshell clam, *Mya arenaria,* from 22 May to August 29, 2003 at an intertidal mudflat in Cutler, Maine. Experiment was designed to assess the interactive effects of stocking density (660 versus 1,320 m^{-2}) and the presence or absence of strips of mesh netting (4.2 mm aperture) surrounding the periphery of experimental units on clam growth.

Source of Variation	df	SS	MS	F	Pr > F
Rim of Netting	1	0.000	0.000	0.00	0.9948
Density	1	0.001	0.001	0.05	0.8174
Netting × Density	1	0.047	0.047	2.47	0.1331
Block (Netting)	18	0.441	0.025	1.17	0.3288
Density × Block (Netting)	18	0.340	0.019	0.90	0.5775
Error	38	0.794	0.021		
Total	77	1.623			

(n = 2 or 1 depending on clam survival).

METHODS

Euspira studies—*Experiment IV August 1986 to June 1987*

Because Commito's (1982b) analysis of moon snail predation on softshell clams was indirect (age-specific survivorship estimates and size distributions of living and dead animals from samples taken near the high tide mark of a flat in eastern Maine on three dates), a field experiment was designed to test directly whether clams >30 mm SL attain a size refuge from *E. heros* attack. The intertidal study site, Hinckley Point (44°54.68′N; 67°12.21′W), is at the confluence of the Dennys and Hardscrabble River near Dennysville, Maine. This site is approximately 12 km (Euclidean distance) from the site in Lubec (Federal Harbor: 44°51.34′N; 67°04.72′W) where Commito (1982b) conducted his sampling. Wild softshell clams (15–51 mm SL) were dug from the immediate vicinity of Hinckley Point and 94 or 188 uniquely marked individuals were added to 0.25 m^2 plots (n = 4 replicates per density treatment) on August 4, 1986. Plots were marked with a wooden stake in each corner. Clams were grouped into four discrete size classes, which represented the natural distribution of clams at Hinckley Point (15–20 mm = 21%; 21–30 mm = 47%; 31–40 mm = 16%; 41–51 mm = 16%), and pushed into the sediments far enough to cover the posterior margin of each individual. Plots were revisited on June 11, 1987, when all live and dead clams were removed and measured (SL) to the nearest 0.1 mm with Vernier calipers. Clams that had been attacked by moon snails had an obvious countersunk hole (or sometimes two) usually near the umbo of one of the valves. The mean borehole diameter from each dead clam was measured using a dissecting microscope with an ocular micrometer by measuring the greatest diameter of the hole and then taking a second measurement perpendicular to the first.

Because of the large number of dead clams with drilled valves, a laboratory trial was designed to determine the relationship between moon snail size and the diameter of the borehole it drills in the valves of its softshell clam prey to estimate size of predator in the field experiment. The study was conducted at BIRSH in late summer 1987. Twenty-one *Euspira* (SH = spire to apex; size range = 9–24 mm) were collected from Weir Cove (44°48.70′N; 67°08.26′W), an intertidal flat in Whiting Bay, approximately 12 km from Hinckley Point. One moon snail and five clams (size range = 16–52 mm SL) were added to each of 21 plastic boxes (10 cm × 10 cm × 6 cm deep) containing poorly sorted beach sand to a depth of 5.5 cm. Each box was covered with nylon window screening and individual containers were placed in running seawater (temperature = 14–15°C) for a two-week period. At the end of the trial, all *Euspira*, *Mya*, and boreholes were measured. To increase the scope of this relationship, a second laboratory experiment was conducted beginning on September 10, 1987. Four large moon snails (size range = 57–70 mm) were collected from the lower intertidal at Mill Cove (44°52.58′N; 67°09.71′W), also in Whiting Bay, and 5.2 km from Hinckley Point. One moon snail and ten clams (size range = 27–77 mm SL) were added to each of four 60-L aquaria containing 15 cm of poorly sorted beach sand and placed into running seawater (temperature = 15–17°C). Measurements of predator, prey, and mean borehole diameter were made as described above.

On October 22, 1987, 20 benthic cores (A = 0.02 m^2) were taken near the upper intertidal at Federal Harbor in the vicinity where Commito (1982b) had sampled from 1977–1979. Core samples were sieved through a 0.5-mm mesh. The SL of each *Mya* with a bored valve and its borehole diameter was measured (as described above), and then the *Euspira*-borehole relationship was used to estimate the size frequency distribution of moon snail predators at Federal Harbor.

Euspira studies—*Experiment V. June to September 1993*

To assess how moon snails respond to increasing juvenile clam density along a tidal gradient, a field test at a mudflat near Bell Farm Cove in Edmunds, Maine (Whiting Bay: 44°49.33′N; 67°09.24′W) was initiated on June 22, 1993. Plastic plant pots (as described earlier) were used as experimental units that were arrayed in a single 5 × 6 block at each of 3 tidal heights (high, mid and low). Within each block, hatchery-reared juvenile softshell clams (mean SL = 8.9 ± 0.62 mm; range = 4.2–15.3 mm) were added to the open enclosures at one of two stocking densities (12 or 24 clams per unit, or 660 or 1320 m^{-2}, respectively). Five replicates of each of the six treatments (a = 3 tidal heights × b = 2 densities) were removed from the flat on July 22, August 22 and September 20, 1993. The contents of each experimental unit were sieved through a 2-mm mesh. The initial and final SL of all clams with countersunk boreholes, typical of *E. heros* attack, was measured to the nearest 0.1 mm using Vernier calipers. Mean borehole diameter of each drilled valve was measured using a dissecting microscope with ocular micrometer. An arcsine transformation was applied to the mean percent dead drilled, and then a model I 3-factor ANOVA was performed to test for treatment effects. In addition, the *Euspira*-borehole relationship (as described earlier) was used to estimate size of moon snail preying on clams and whether predator size varied as a function of tidal height, stocking density and sampling date.

Carcinus studies—*Experiment VI. October 1993*

C. maenas has been presumed to be the major crustacean predator in most field experiments conducted in eastern Maine (Beal 1994, Beal et al. 2001, Beal & Kraus 2002). It is not difficult to identify general mortality agent based on shell damage in soft-shell clams. Typically, highest predation rates can be attributed to crab attack that is inferred from crushed and/or chipped valves. Field investigations have shown that crab predation is highly seasonal and varies along a tidal gradient (Beal et al. 2001). Predation rates caused by large crustaceans are relatively low at all tidal heights prior to August. From August until the beginning of October, rates are the highest observed during the year. Mortality of clams (ca. 12.4 mm SL) caused by crustacean predators was <20% for animals held in open enclosures near the high- and mid-water mark at an intertidal flat near Jonesport, Maine from April 6 to December 13, 1996 (Beal et al., 2001). However, mortality rates varied from 40% to 50% for animals in open enclosures near the low tide mark over the same period. Protective netting enhanced clam survival only at the lowest tidal elevation where difference in mean survival between units with and without the predator deterrent mesh was nearly 30% ($\overline{x}_{protected}$ = 91.1 ± 4.5% versus $\overline{x}_{unprotected}$ = 63.3 ± 9.7%, n = 120, P < 0.0001).

Beal and Kraus (2002) examined the interactive effects of protective netting, initial clam size and stocking density on clam survival in separate studies at two intertidal locations near Jonesboro and Cutler, Maine. From June 1990 to June 1991, crushing predators accounted for 33.6% and 20.3% of losses of clams initially 8.5 and 11.8 mm SL, respectively, in open enclosures. From April to October 1991, losses of clams initially 14.6 mm from open enclosures ranged from 15% to 20%. Until now, however, identification of which crustacean species attacks juvenile clams in the intertidal has been indirect, based solely on shell damage.

To identify which crushing predators are active on clam flats during periods of tidal inundation, a passive trapping study was conducted at an intertidal flat in Cutler, Maine (see earlier) during October 1993. Vinyl-coated, wire lobster traps (61 cm × 55 cm × 38 cm), baited with salted herring (*Clupea harengus* L.), were placed outside and inside each of five sea grass beds (area of each bed ranged from 150–250 m^2). Distance between traps from outside to inside a bed was no more than 15 m. The test was initiated at low tide on October 1 and traps were checked irregularly (on 10 dates) at periods of low water until October 21. New bait was added to each trap on each sampling date, except the last. When a crab was found within a trap, it was measured (greatest carapace width to the nearest 0.1 mm) and its sex recorded. Before releasing trapped crabs, the dactyl from each pair of fourth walking legs was excised. This provided a common mark that I used to distinguish animals caught more than once.

RESULTS

Euspira—*Experiment IV*

Of 1128 clams transplanted initially to the eight field plots in August 1986, only 600 were recovered (47% were missing), and of these, 215 were alive and 385 were dead. Growth rates were extremely slow with animals >40 mm exhibiting no significant shell growth and animals <40 mm exhibiting increases in SL between 3 and 5 mm. Approximately 77% (296) of the total number recovered dead had been drilled by *Euspira* (Table 5). Moon snails did not demonstrate a density-dependent response to their prey based on total number per plot or initial size (G = 2.8, df = 3, P = 0.43) but did show a preference for clams between 31 and 40 mm SL. A comparison of the initial size distribution versus the size distribution of drilled individuals (Fig. 8) reveals that *Euspira* fed selectively on different size clams (G = 84.9, df = 3, $P < 0.0001$). Examination of the expected frequencies within the 2 × 4 contingency table revealed that the proportion (6%) of drilled clams in the smallest size category (15–20 mm) is three times lower than expected (18%) and the proportion (38%) of drilled clams between 31–40 mm is nearly double the expected frequency (20%).

The relationship between mean borehole diameter and snail size (Fig. 9), allows one to estimate the size of snails drilling clams in the field (Fig. 10). Moon snails at Hinckley Point flat ranged in size from approximately 10–52 mm in shell height. Nearly 70% of the moon snails preying on *Mya* were between 20–30 mm. Mean snail size ± 1 SE was 24.4 ± 0.30 mm (n = 296). Conversely, moon snails at Federal Harbor were smaller ($\overline{x}$ = 11.9 ± 0.29 mm), and ranged from 8–29 mm (n = 94). The two distributions were significantly different ($P < 0.0001$; G-test of independence).

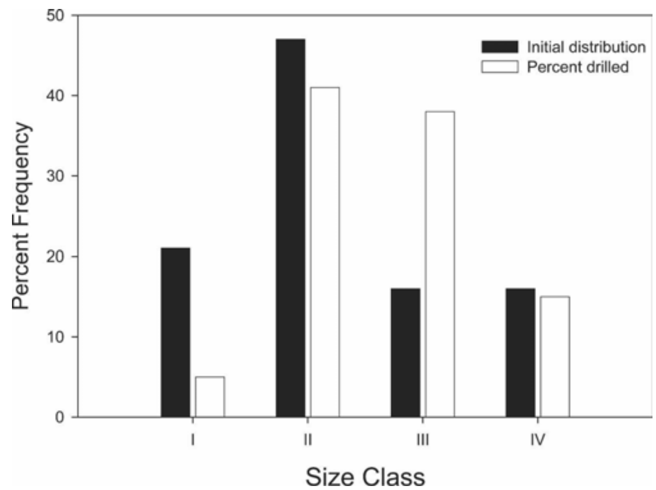

Figure 8. Initial size-frequency distribution of clams used in a field experiment from August 4, 1986 to June 11, 1987 and the distribution of clams with a bored valve from moon snail, *Euspira heros*, attack Size classes of clams (SL) are: I = 15–20 mm; II = 21–30 mm; III = 31–40 mm; IV = 41–51 mm. The two distributions are different (*P* < 0.0001) indicating that snails prefer a particular size *Mya*. Clams in size class III were drilled at a rate that was nearly double than what was expected (*P* < 0.05; G-test of independence). Conversely, clams in size class I were drilled less frequently than expected.

Euspira—*Experiment V*

From June to July 1993, 71.5 ± 8.13% (n = 30) of the *M. arenaria* juveniles were recovered dead with drilled valves, and this rate increased through time (P = 0.0066). There was no difference in mean percent with drilled valves from the final two sampling dates (81.7 ± 4.06%, n = 60; P = 0.1403). Mean snail size varied significantly with date, tidal height and stocking density (Table 6). Snails were smaller in June (16.5 ± 1.06 mm, n = 29) than they were in July and August (17.6 ± 0.89 mm, n = 60), decreased in size from the high (20.6 ± 0.94 mm, n = 30) to the mid and low tide mark (15.5 ± 0.52 mm, n = 59) and increased in size with increasing intraspecific clam density (mean SH of snails in units stocked at 660 vs. 1, 320 m^{-2} was 16.5 ± 0.90 mm vs. 17.9 ± 1.02 mm).

TABLE 5.

Fate of *Mya arenaria* at two densities (1× = 94 m^{-2}, 2× = 188 m^{-2}) from 4 August 1986 to June 11, 1987 at Hinckley Point Flat, Dennysville, Maine. *n* = number of clams at the beginning of the experiment, A = percent recovered Alive, UV = percent recovered dead with Undamaged Valves, DV = percent recovered dead with countersunk, Drilled Valves, CV = percent recovered dead with Chipped or Crushed Valves. One-way ANOVA on the angular-transformed mean percent with drilled valves (DV) failed to detect significant differences due to stocking density.

PLOT	*n*	A	UV	DV	CV	M
1	94	5	13	39	0	43
2	94	12	6	43	1	38
3	94	12	6	37	0	45
4	94	29	5	9	0	57
1	188	16	6	22	0	56
2	188	30	9	28	1	32
3	188	12	13	29	2	44
4	188	27	2	13	1	57

M = percent Missing.

Carcinus—*Experiment VI*

Thirty-one green crabs (mean carapace width, CW = 72.6 mm) and 22 rock crabs, *Cancer irroratus* Say (mean CW = 97.6mm), were caught in the traps during the test interval. All crabs were male, and no individual was caught more than once. Fewer crabs were caught near the end of the month than at the beginning, and each species demonstrated a preference for one location over another (P = 0.02). Green crabs were 4.1× more likely to be caught inside eelgrass beds than outside them, whereas

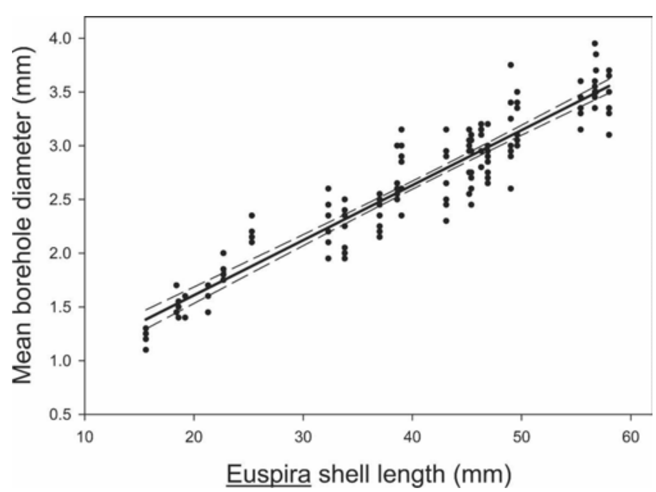

Figure 9. Relationship between mean borehole diameter (in the valves of *M. arenaria*) and size of moon snail predator. Dotted lines represent 95% confidence intervals. Y = 0.058 + 0.0512 X, *n* = 138, r^2 = 0.884, *P* < 0.0001.

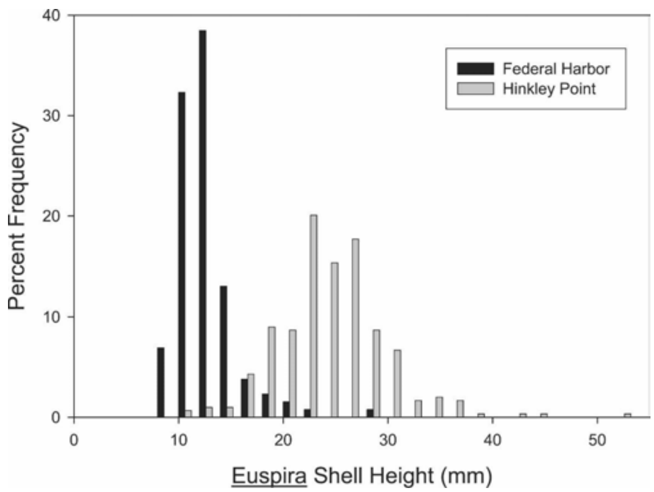

Figure 10. Estimated size-frequency distribution of moon snails from Federal Harbor, Lubec, Maine (*n* = 94), where Commito (1982b) concluded that soft-shell clams reach a refuge from moon snail attack after they attain a SL of 30 mm, and from Hinckley Point, Dennysville, Maine (*n* = 296). Both distributions were created by measuring the mean borehole diameter of clams collected from both sites and then using the linear equation relating borehole diameter to snail size (see legend of Fig. 9).

rock crabs were 2.7× more likely to be found in traps on the unvegetated muddy sediments. The results indicate that assigning all crushing and chipping damage to green crabs is not appropriate and that it is possible that rock crabs prey on small softshell clams in the intertidal zone during periods of tidal inundation.

DISCUSSION

In Maine, USA, intertidal populations of softshell clams are a public resource that is comanaged by the local community in cooperation with State government and its regional shellfisheries biologists. Two decades ago, approximately one-half of coastal communities along the Maine coast actively managed their softshell clam fishery through local ordinances. Today, that percentage is 70%, and, although most of these communities participate in some form of active management efforts to enhance stocks (e.g., clam transfers, netting to encourage spatfall, planting hatchery-reared seed), all benefit from restricted, or limited entry, which results in an approximate 15% higher yield for harvesters than those in communities without local management plans (Townsend 1985).

TABLE 6.

Analysis of variance on the untransformed mean size (shell height) of moon snails (*Euspira heros*) attacking hatchery-reared juveniles of *Mya arenaria* from June 22 to September 20, 1993 at an intertidal flat near Bell Farm Cove, Edmunds, Maine. Clams were stocked at one of two densities (660 or 1,320 m^{-2}) at three tidal heights (high, mid, low) and samples on three dates: July 22, August 22, and September 23. A decision rule of $\alpha' = 0.0253$ was used for each single degree-of-freedom, orthogonal contrast involving sampling date and tidal height.

Source of variation	df	SS	MS	F	Pr > F
Sampling date	2	30.03	15.01	3.70	0.0297
(1) June versus July & August	1	29.73	29.73	7.32	0.0086
(2) July versus August	1	0.30	0.30	0.08	0.7846
Tidal height	2	525.69	262.85	64.68	<0.0001
(1) High versus mid & low	1	524.27	524.27	129.01	<0.0001
(2) Mid versus low	1	1.42	1.42	0.35	0.5559
Date × tidal height	4	27.95	6.98	1.72	0.1552
Density	1	48.56	48.56	11.95	0.0009
Date × density	2	9.65	4.83	1.19	0.3109
Tidal height × density	2	5.01	2.51	0.62	0.5425
Date × tidal height × density	4	8.28	2.07	0.51	0.7289
Error	71	288.53	4.06		
Total	88	943.70			

(n = 5).

Clam Transfers

Today, approximately 44% of Maine communities that manage their *M. arenaria* stocks participate in some form of clam transfer program (ME DMR 2005) by harvesting clams from areas of high density and replanting them in areas with lower clam abundance (usually lower on the shore). To date, however, only anecdotal information exists about the efficacy of these activities. Generally, seed clams (animals <50.8 mm SL that typically range from 38–45 mm SL) are dug by hand by groups of clammers, and then immediately (or within 24 h) replanted by broadcasting the animals from a boat at high tide into a closed intertidal area. Clams may take up to 72 h to reburrow because burrowing rate depends on clam size and seawater temperature (Zwarts & Wanink 1989, Zaklan & Ydenberg 1997). At present, no shellfish committees apply netting to the reseeded area to deter predators. Further, no community chooses to follow the fate of the transferred animals. Instead, success is measured by the number or volume of clams transferred during any given effort. Although a single field test on clam transfers was conducted and generalizations should not be made, results presented here suggest that if communities choose to participate in clam transfer programs, they can improve production in the reseeded areas simply by using protective netting. This would have to be done at low tide when it would be possible to secure the netting around the seeded plot, however. Netting did not meet the criteria of statistical significance in this study, but did result in an overall 120% increase in final mean density compared with the density of transferred clams in plots without netting. It is unclear, however, whether the netting acted only to retain clams in the seeded areas or improve seed survival by deterring predators. Another benefit of using the plastic, flexible netting was that it enhanced wild recruitment 3-fold compared with control plots.

The transfer field experiment was conducted to provide several biological parameters to help the city of Eastport's shellfish conservation committee decide what steps it should take regarding this management option. No cost-benefit analysis was done; however, in eastern Maine, where large numbers of adult clams occur in the extreme upper intertidal zone, and where growth rates are very slow and legal sizes may be attained only after 10 years (Fig. 4), these efforts may be cost-effective and necessary. Results from this study suggest that growth rate of clams from these high intertidal areas is plastic as they assume rates of shell accretion that is typical of the area to which they are transferred (see also Dow & Wallace 1961). Transfer efforts may allow some communities to harvest clams legally that they may not be able to do otherwise. Typically, clams in these high intertidal areas are not harvested and left to grow and presumably reproduce. It is unknown, however, whether these "refuge populations" act as natural spawner sanctuaries (sensu McCay 1988), and if clam transfer efforts were to increase whether this would have any effect on natural recruitment in that region.

Shell growth

Growth of infaunal and epifaunal bivalves in the intertidal zone typically is related to submergence time, varying inversely with tidal height (Mead & Barnes 1904, Newcombe 1935, Jordan & Valiela 1982, Vincent et al. 1989, Stiven & Gardner 1992). Several investigations, however, have shown that although bivalve growth may be faster lower on the shore than in the upper shore area, rates do not necessarily parallel directly submergence times (Peterson & Black 1987, 1988, Beal et al. 2001). The yearlong study at Carrying Place Cove in Eastport (April 1998–1999) demonstrated that clams at the mid and upper intertidal zones grew faster than animals at the extreme low intertidal. Only 5 of 216 clams planted in open plots near the low intertidal survived (2.3%), and these grew extremely slow (e.g., 1.9 ± 1.5 mm SL). Survival was significantly higher in plots near the mid and upper intertidal, where growth rates followed expected patterns (Fig. 4). Why was growth so slow among clams in the lower intertidal zone where they were submerged nearly 100% of the time? Intraspecific competition can be ruled out because survival rates were so low. Interspecific competition may explain partially this result, because the plots were adjacent to subtidal beds of blue mussels, *Mytilus edulis* L. Another factor may have been disturbance caused by the predatory activities of the moon snail, *Euspira heros*. After measuring the borehole diameters of the drilled clams and using the *Euspira*-borehole diameter equation (Fig. 9), it was determined that the mean snail size preying on the clams at the mean low tide level was 40.0 mm. Reductions in shell growth have been attributed to predators in several field studies. For example, the shell growth of hard clams, *Mercenaria mercenaria* (L.) was nearly 100% slower when animals were exposed to whelk attack (Nakaoka 2000). Similarly, Peterson and Black (1993) observed a 50% reduction in growth of *Katelysia scalarina* Lamarck and *K. rhytiphora* Lamarck in full cages versus open enclosures in Western Australia that was presumably because of increased disturbance by a predatory seastar that had gained entrance to the protected cages.

The growth of juvenile softshell clams in protected and unprotected experimental units was followed in experiments conducted in Jonesport and Addison, Maine. Neither test demonstrated a significant difference in final mean SL between the two treatments, a result consistent with Beal and Kraus (2002). Results from the Addison study indicate the importance of spatial variability in clam growth rates as juveniles at two of the sites exhibited significantly faster growth (20% difference in mean SL) than those at the other two sites. Differences in final SL were not associated with variation in tidal height as experimental units at all four sites were deployed at a single tide level. Spatial differences in bivalve growth may be related to differential microalgal concentrations in the water column that have been found to differ dramatically between adjacent sites (Posey et al. 2002, Carmichael et al. 2004), a reflection of spatial differences in biological disturbance, or differences in sediment composition (Newell & Hidu 1982).

A small percentage of clams in the Addison study attained legal size in one growing season (May to November). From May to November 2001, clams added an average 27.2 ± 1.17 mm ($n = 22$) and 25.5 ± 1.71 mm ($n = 22$) of new shell at Eastern Harbor and Three Brooks, respectively. These growth rates are faster than reported for this species anywhere in Maine (Dow & Wallace 1953, Spear & Glude 1957, Newell & Hidu 1982, Commito 1982b, Beal 1994). In addition, these rates are faster than those reported for 0-y class individuals of *Mya* in northern Massachusetts (Brousseau 1979).

Previous field studies with hatchery-reared juveniles of *M. arenaria* (Beal 1994, Beal et al. 2001, Beal & Kraus 2002) assumed that the rim of netting used along the periphery of the small experimental units to enclose clams (but still allow predators access to the clams in the unit) did not affect clam growth. Although results presented here and elsewhere (Beal et al. 2001) have demonstrated that completely covering the top of experimental units with protective netting has no significant effect on clam growth, Experiment III a & b tested the assumption explicitly. Those results revealed that published growth rates are not confounded by the addition of a strip of netting projecting 4–5 cm above the surface of the sediments. Relative growth rate and final mean SL were nearly identical in both tests.

Predation

The three field experiments involving moon snails and green crabs add to an extensive literature on the importance of predation in controlling populations of juvenile and adult softshell clams in Maine (Commito 1982a, b, Thiel 1997, Ambrose et al. 1998, Beal et al. 2001, Beal & Vencile 2001, Beal & Kraus 2002, Whitlow et al. 2003). Although moon snails, *Euspira heros*, occur along the entire coast of Maine, their numbers (as estimated by their predatory activities associated with *Mya*) seem to be greater in eastern Maine than elsewhere (Beal, pers. obs.). Softshell clam seeding activities using cultured juveniles produced at BIRSH that have occurred in each coastal county of Maine (1987–2005) and mortality caused by moon snails is problematic only in eastern Maine (Washington County). By analyzing size-frequency data of both predator and prey populations at Federal Harbor in Lubec, Maine from 1977–1979, Commito (1982b) demonstrated that soft-shell clams escape moon snail predation by growing relatively quickly (over 5 y) to a refuge size of 30-mm SL. Moon snails at the upper intertidal of Federal Harbor rarely exceeded 30 mm in shell height.

On numerous occasions in 1984 and 1985 while inspecting intertidal flats in Cobscook and Whiting Bays, many dead, drilled *Mya* were discovered that were >50 mm SL. The experiment at Hinckley Point from 1986–1987 demonstrated that an absolute size refuge of 30 mm from moon snail attack may be common at some intertidal flats, but not at others (Fig. 10), because moon snail size may vary along a tidal gradient. *Euspira* occurs both in the intertidal and subtidal in Maine waters. Larger moon snails (up to 100 mm in shell height) are found below mean low water, whereas smaller animals are found from mean low water to the high water mark (B. Beal, pers. obs.). It is likely that a gradient of refuge sizes exist for *Mya* from *E. heros* attack that increases in SL from the upper to lower shore levels. Besides the Hinckley Point study that indicated more clams in the 31–40 mm size range fell victim to moon snails than was expected by random chance alone, high mortality rates occurred in clams >30 mm SL in Eastport (Experiment II) at the lowest tidal level from 1998–1999. Subsequent analysis of mean snail size using the *Euspira*-borehole diameter relationship (Fig. 9) showed that snails preying on clams at that site averaged 40 mm in shell height. Similar analysis of boreholes in drilled *Mya* from the Hinckley Point experiment showed that some moon snails were as large as 52 mm in shell height.

Moon snails are voracious predators of juvenile softshell clams. The study conducted at Bell Farm Cove in 1993 demonstrated that approximately 70% of juveniles <10 mm SL were preyed on by *E. heros* during the first month, from June to July. Although mean snail size was <20 mm at all tidal heights at that site, animals were significantly larger nearer the high versus mid and low tide levels. Maximum snail size was estimated to be 30 mm SH. Vencile (1997) determined that moon snails drill clams that are approximately similar in SL to their shell height. In this study, a similar relationship existed (Snail size $= 10.37 + 0.689 \times$ SL, $n = 1262$); however, clam SL explained only 6% of the variation in snail size.

Green crabs, *C. maenas*, are perhaps the best known, and most widely studied, predator of juvenile and adult soft-shell clams in Maine and the northeast United States (Glude 1955, Ropes 1968, Hunt & Mullineaux 2002, Whitlow et al. 2003, Hunt 2004). Intertidal field studies in eastern Maine have demonstrated the efficacy of excluding large crustaceans from experimental units containing softshell clam juveniles (Beal 1994, Beal et al. 2001, Beal & Kraus 2002). For example, between April and September, clam survival in the low intertidal zone at Flake Point Bar, Jonesport, Maine varied from 83% to 103% higher in protected versus open experimental units (Beal et al. 2001). Mean losses exceeded 50% in open enclosures, and, because *C. maenas* was found in some open enclosures, this predator was assigned as the mortality agent. The trapping study conducted in Cutler, Maine reveals that *Cancer irroratus* does forage intertidally during periods of tidal inundation. It remains to be seen whether differences in *Mya* shell damage exist between these two large crustacean predators.

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