

## **Experimental Trials on the Nursery Culture, Overwintering, and Field Grow-Out of Hatchery-Reared Northern Quahogs (Hard Clams), *Mercenaria mercenaria* (L.), in Eastern Maine**

Author(s) :Brian F. Beal, George Protopopescu, Katy Yeatts and Joseph Porada

Source: Journal of Shellfish Research, 28(4):763-776. 2009.

Published By: National Shellfisheries Association

DOI:

URL: <http://www.bioone.org/doi/full/10.2983/035.028.0405>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## EXPERIMENTAL TRIALS ON THE NURSERY CULTURE, OVERWINTERING, AND FIELD GROW-OUT OF HATCHERY-REARED NORTHERN QUAHOGS (HARD CLAMS), *MERCENARIA MERCENARIA* (L.), IN EASTERN MAINE

BRIAN F. BEAL,<sup>1,2\*</sup> GEORGE PROTOPODESCU,<sup>2</sup> KATY YEATTS<sup>2</sup> AND JOSEPH PORADA<sup>3</sup>

<sup>1</sup>University of Maine at Machias, 9 O'Brien Avenue, Machias, ME 04654; <sup>2</sup>Downeast Institute for Applied Marine Research and Education, 37 Wildflower Lane, Beals, ME 04611; <sup>3</sup>Egypt Bay Seafarms, 698 Stream Road, Winterport, ME 04614

**ABSTRACT** The easternmost commercial population of hard clams, *Mercenaria mercenaria*, in Maine was discovered recently near the low intertidal in Goose Cove, in the town of Trenton (Hancock County). A fast- and slow-growing morph was identified that reaches commercial size (50.8 mm shell length) in 4 y and 5 y, respectively. Fast-growing individuals were selected as broodstock, and conditioned to spawn at the Downeast Institute. The fate and growth of cultured juveniles was followed for 5 mo beginning in July 2006 at 4 stocking densities (2,500–10,000 animals/1.1 m<sup>2</sup> floating, nylon window screen-lined tray;  $n = 20$ ) at a coldwater field nursery approximately 60 km east of Trenton, in the town of Beals, ME (Washington County). Survival was nearly 100%, and growth was density dependent, with animals attaining a final mean shell length  $\pm 95\%$  confidence interval of  $8.4 \pm 0.13$  mm and  $7.6 \pm 0.218$  mm in the lowest and highest density treatments, respectively. In November 2006, cultured seed was separated into 2 sizes (large,  $8.7 \pm 0.2$  mm; small,  $5.1 \pm 0.2$  mm) and overwintered in window-screen bags (0.2 m<sup>2</sup>) at densities ranging from 0.6–1.6 kg (large) and 0.5–1 kg (small), representing approximate densities ranging from 3,360–15,510 individuals per bag. Bags were placed on horizontal shelves within modified lobster traps (overwintering containers) that were added to a 35,000-L tank receiving ambient seawater for 177 days until May 2007. Seawater temperatures during this interval ranged from  $-1$ – $10^\circ\text{C}$ . Survival rates exceeded 99%, and no negative effects resulting from stocking density were observed. Hatchery seed was transplanted in May 2007 to the lower intertidal at Goose Cove and a second intertidal location approximately 30 km east of Beals at Duck Brook Flat, in the town of Cutler, and the fate and growth of these juveniles was followed for 6–7 mo. Survival was independent of planting densities (330–1320 individuals/m<sup>2</sup>), and predator netting did not enhance survival compared with controls without netting. Growth was seasonal, with the greatest incremental shell increases occurring between early July and late September. Growth rates varied between planting locations, with clams adding approximately 10 mm shell length at Goose Cove between May and December (initial shell length, 8.2 mm; final shell length, 17.9 mm) and approximately 5 mm shell length at Duck Brook Flat between June and November (initial shell length, 9.3 mm; final shell length, 14.3 mm). Hard clam farming in eastern Maine may help to diversify a wild shellfish industry that is currently in decline for most species except lobsters; however, additional efforts are needed to explore alternative grow-out sites and methods to enhance growth rates.

**KEY WORDS:** *Mercenaria mercenaria*, northern quahogs (hard clams), Maine, culture, overwinter, growth, survival

### INTRODUCTION

The northern quahog, or hard clam, *Mercenaria mercenaria*, ranges from Prince Edward Island and the southern Gulf of St. Lawrence, Canada, to the central coast of eastern Florida (Dillon & Manzi 1987, MacKenzie et al. 2002, LeBlanc et al. 2005). Ingersoll (1887) described a discontinuity in the distribution of hard clams between New Brunswick and the Maine/New Hampshire border, except in a few sheltered bays in southern Maine. These locations were identified by Dow & Wallace (1951) and Gustafson (1955) as areas primarily limited to Maquoit Bay (Brunswick) and Quahog Bay (Harpwell), in Cumberland County (Fig. 1), where hard clams exist in the lower intertidal (B. Beal, pers. obs.). One published report exists of 2 live individuals from the northwest side of Mount Desert Island, in Hancock County (Proctor 1929); however, no published accounts of wild populations of hard clams have been reported between southern Maine and St. Andrews, New Brunswick, where *M. mercenaria* occurs in Sam Orr Pond (Dillon & Manzi 1992).

In Maine, a small wild fishery has existed in Casco Bay since at least the 1930s (Dow & Wallace 1951). Cultured hard clams have been reared in the Damariscotta River (Lincoln County;

$43^\circ 58.69' \text{N}$ ,  $69^\circ 34.30' \text{W}$ ; B. Scully, Edgcomb, ME, pers. com.), and as far north as the Bagaduce River (Hancock County;  $44^\circ 25.31' \text{N}$ ,  $68^\circ 44.37' \text{W}$ ; J. Leach, Brooklin, ME, pers. comm.). Recently, a self-sustaining population of hard clams was discovered at Goose Cove, Trenton (near Mount Desert Island, ME; Fig. 1), where commercial harvests have been occurring for nearly 2 decades by one of us (J. Porada, pers. obs.). Anecdotal evidence suggests that the quahogs in that vicinity arose from wild seed transplanted from Casco Bay to Sullivan Harbor in Frenchman's Bay (Hancock County;  $44^\circ 30.65' \text{N}$ ,  $68^\circ 12.76' \text{W}$ ) during the mid-1950s by members of Maine's Department of Sea and Shore Fisheries (currently, the Maine Department of Marine Resources) (D. E. Wallace, Brunswick, ME, pers. comm.). Those efforts coincided with the northern migration of green crabs, *Carcinus maenas*, that were decimating softshell clam populations in southern and midcoast Maine (Glude 1955, Grosholz & Ruiz 1996), as managers were attempting to create a new bivalve fishery in far eastern Maine to ameliorate the effects of the invasive crabs.

Because no published information exists about this northeastern population of hard clams, we examined shell growth of wild individuals harvested from Goose Cove to establish the rate at which animals reach commercial size (hinge width, or thickness, of 25.4 mm, or shell length of 50.8 mm). In addition, because the relative economic value of hard clams is more than

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

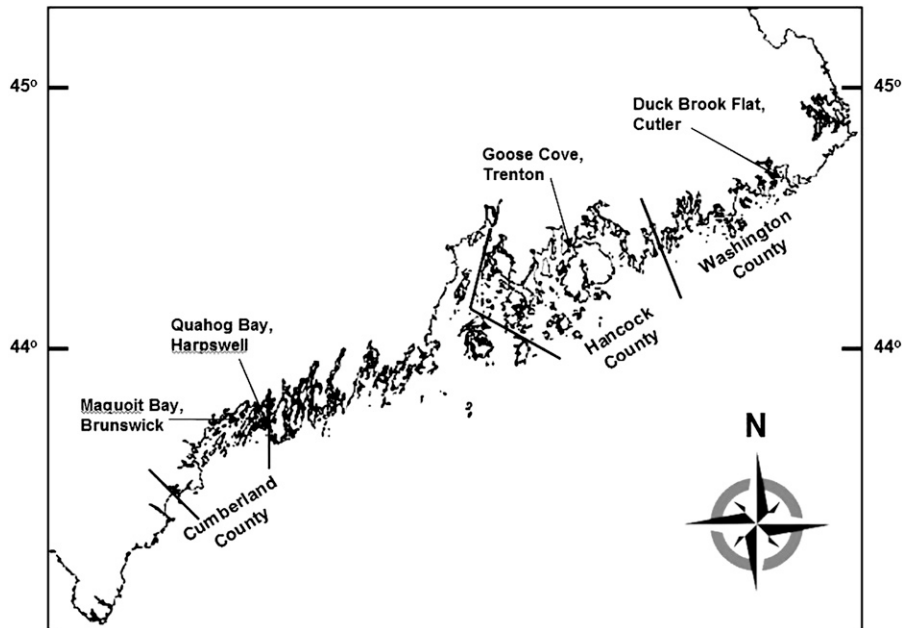


Figure 1. Maine coast with coastal counties labeled. A self-sustaining population of hard clams has been harvested commercially at Goose Cove, Trenton, for the past 2 decades. The fate and growth of F1 juveniles cultured from Goose Cove broodstock was assessed at Goose Cove and another site approximately 90 km east in Cutler at Duck Brook Flat in spring 2007.

twice that of other commercial bivalve species harvested in this region (i.e., softshell clams, *Mya arenaria*; blue mussels, *Mytilus edulis*; mahogany quahogs, *Arctica islandica*) (J. Markos, Maine Shellfish, Ellsworth, ME, pers. comm.), we investigated several biotic and abiotic factors affecting survival and growth of juveniles cultured from eastern Maine broodstock. Specifically, we examined growth and survival of cultured juveniles reared from parental broodstock taken from Goose Cove across several stocking densities in a field-based floating nursery (sensu Beal 2005), overwinter mortality using a technique developed for *M. arenaria* (Beal et al. 1995), and seasonal growth and survival at 2 intertidal sites in eastern Maine.

Hard clams are commercially cultured in every state along the east coast of the United States from Massachusetts to Florida. Economic impact of cultured hard clam activities has been estimated in some states. For example, Florida clam companies had nearly \$22 million in sales to wholesalers, restaurants, retailers, and other consumers in 1999 that had an overall impact of \$55 million to Florida's economy (Philippakos et al. 2001). In Virginia in 2004, Eastern Shore hard clam farm sales were associated with 380 full-time jobs and an economic output of nearly \$49 million (Murray & Kirkley 2005). In New York, where wild hard clam harvests fell 82% between 1976 and 2005, cultured hard clams have had value in rebuilding commercial stocks as towns across Long Island have developed shellfish management programs that include municipal hard clam hatcheries (Rivera 2007). In Maine, 3.7 mt of wild hard clams were harvested in 2007 worth \$45,412 (Maine Department of Marine Resources 2007). During the early 1950s, the annual harvest in the Casco Bay region averaged nearly 200 mt for several years (Dow & Wallace 1955). Although softshell clams are ubiquitous and commercially important along Maine's coast, landings in eastern Maine have fallen to record lows resulting from the lack of natural pro-

duction (Congleton et al. 2006). If cultured hard clam juveniles will grow and survive in the lower intertidal of eastern Maine, then it may be possible to create a novel culture fishery and/or for individuals to participate in commercial clam farming ventures.

Here, we describe the growth of a wild population of *M. mercenaria* sampled from the lower intertidal at Goose Cove, Trenton, ME, and investigate growth and survival of cultured juveniles produced from these wild stocks at different stocking densities in a field-based nursery located in Beals, ME, in overwintering trials (sensu Beal et al. 1995), and in short-term field grow-out trials at 2 eastern Maine intertidal locations.

## METHODS

### Wild Clam Growth in Trenton, ME

On December 7, 2005, 111 animals were collected (shell length range, 21.7–97.9 mm) haphazardly from areas below the mean low water mark at Goose Cove, Trenton, ME (44°25.80'N; 68°23.11'W) using commercial hoes (sensu Robinson and Rowell 1990) to determine growth rate of a variety of sizes of wild individuals. This cove represents the easternmost area in Maine where this bivalve is harvested commercially (J. Porada, pers. obs.). Animals were steamed, meats removed, and the right valve of 16 individuals was cut from the umbo to the ventral margin using an Isomet (Buehler Ltd., Lake Bluffs, IL) low-speed, diamond-tipped saw. The number of times that internal lines formed discrete bands within each shell was examined grossly and then compared with the number of distinguishable external lines. It was not necessary to use the acetate peel method (as described in Peterson et al. [1983]) to discern internal lines because the recurring bands were dark (generally purple), discrete, and separated by an area of smooth,

white shell. We assumed that the dark banding pattern, similar to that described in the shells of *Mercenaria* from New Jersey (Grizzle & Lutz 1988) and Rhode Island (Henry & Cerrato 2007), represented a slowing of growth; hence, a winter check.

#### Broodstock Conditioning, Larval Rearing, and Field Nursery Grow-out Trials

Approximately 40 broodstock (shell length range, 50–65 mm) were collected in January 2006 from Goose Cove, Trenton, ME, from animals exhibiting the fastest growth (widest external lines; see Results). Animals were taken to the Downeast Institute for Applied Marine Research & Education (DEI), Great Wass Island, Beals, ME (44°28.85'N; 67°35.92'W), where they were placed in 20°C seawater and fed cultured phytoplankton (*Tetraselmis maculata*, CCMP897; and *Thalassiosira weissflogii*, CCMP1336) to condition (sensu Loosanoff & Davis 1950) for 8 wk. Four groups of 15 individuals each were sandwiched between rigid pieces of wire mesh that were held together using nylon cable ties. Ties helped keep a constant pressure on the valves of the hard clams, which were suspended inside gently aerated 500-L tanks at 20°C. Spawning was induced by thermal shock, and larvae were reared for 12 days at 24°C. Larvae and juveniles were fed a mixed diet of *Isochrysis galbana*, CCMP1324; *Chaetoceros mueleri*, CCMP1316; and *C. neogracile*, CCMP1318.

When juveniles reached a size large enough to be retained on window screening (approximately 3 mm shell length), they were moved from the DEI shellfish production center to a nearby nursery field site at Mud Hole Cove (MHC), Great Wass Island, Beals, ME (44°29.15' N, 67°35.17' W; see Beal et al. [1995] for a detailed description of this site). We examined effects of intraspecific stocking density on growth and survival of the hatchery-reared hard clam seed held in floating, flow-through nursery trays at MHC from July 5–6 to November 16, 2006. Air temperatures during this time near the water surface measured at the Jonesport, ME, NOAA buoy, approximately 5 km away from the study site, ranged from 8.5–15.3°C. Surface water temperatures ranged from 7.2–14.4°C, and winds were mainly from the south and south southwest with speeds to 25 kph (Anonymous 2007).

Clam seed were placed into rectangular wooden floating trays (1.2 × 0.9 m) lined with nylon window screen netting (1.8-mm aperture) both on top and bottom, at 1 of 4 densities: 2,500, 5,000, 7,500, and 10,000 individuals ( $n = 20$  replicates per stocking density). Trays were deployed by boat over the course of 2 days in 4 lines of 20 trays (treatments were randomized within each line). Lines were spaced 10 m apart, and trays within the lines were spaced approximately 60 cm apart. The top of each tray was covered with a piece of 1-mm-thick black plastic to prevent seagull (*Larus argentatus*, *L. marinus*) predation that occurs when plastic is not used (B. Beal, pers. obs.). Lines of floating trays were anchored on each end, which helped maintain trays in the same relative position during the field experiment. Trays were monitored regularly to ensure that they did not overturn; however, no maintenance (scrubbing, cleaning, and so forth) was done to any of the trays during the trial. All trays were retrieved from the cove on November 16 and taken to DEI, where they were processed. A random sample (14 g) was removed from each tray. All live and dead animals from each sample were counted, and the shell length of each live clam was measured to the nearest 0.1 mm using Vernier calipers.

#### Overwintering Trials at the Downeast Institute (November 16, 2006–May 13, 2007)

After clams were removed from each nursery tray, they were placed into 1 large group and then sorted into 2 size classes (large:  $\bar{x}_{SL} \pm 95\%$  confidence interval [CI] =  $8.7 \pm 0.2$  mm, minimum = 6.5 mm, maximum = 11.3 mm,  $n = 110$ ; small:  $\bar{x}_{SL} = 5.1 \pm 0.2$  mm, minimum = 2.5 mm, maximum = 7.5 mm,  $n = 100$ ). Large clams were added to 45 × 45-cm bags constructed of nylon window screening (as described earlier) at each of 3 masses (0.6 kg, 1.2 kg, and 1.6 kg, representing approximate densities per bag of 3,360, 6,720, and 8,960 individuals, respectively). Seven bags from each density treatment were added to overwintering containers. Containers were modified commercial lobster traps constructed of vinyl-coated, 14-gauge wire mesh (0.96 × 0.45 × 0.45 m), except instead of opening like a chest freezer, each container opened like a refrigerator. Each container had a series of 8 horizontal shelves that were spaced equidistant from each other. One bag containing clams from a single density was placed on 1 shelf within each container except the bottommost shelf. Two containers were used for each density treatment. Small clams were placed in similar-size bags at 3 different masses (0.51 kg [ $n = 2$ ], 0.72 kg [ $n = 13$ ], and 0.99 kg [ $n = 1$ ], representing approximate densities per bag of 7990, 11,302, and 15,510 individuals, respectively). Two overwintering containers were used to hold the bags of small clams. Density treatments were randomly assigned to positions within each container. On November 16, 2006, all containers were placed into a 35,000-L (15 m long × 1.5 m wide × 1.5 m deep) cement tank at DEI that received ambient, flowing seawater. Containers and bags of clams were removed from the tank and cleaned (sprayed with freshwater to remove silt) 4 times during the 177-day experiment. At the end of the experiment, on May 13, 2007, a 14-g random sample was taken from each bag, and the number of live and dead hard clams was recorded. Seawater temperature in the tank was monitored daily (Fig. 2), and ranged from 10°C on November 16, 2006, to -1°C for nearly 3 wk in February 2007. On May 13, 2007, seawater temperature was 7°C.

#### Field Grow-out Trials

##### Goose Cove, Trenton, ME (May 20 to December 22, 2007)

Cultured juveniles that had been overwintered at DEI were planted below the mean low tide mark on May 20, 2007, in the general vicinity where broodstock had been collected the year before. Initial mean shell length  $\pm 95\%$  CI was  $8.2 \pm 0.15$  mm (shell length range = 4.8–12.0 mm,  $n = 100$ ). Clams were planted at an approximate density of 540 clams/m<sup>2</sup> in rectangular plots ( $n = 14$ ) with dimensions approximately 3.65 × 6.09 m. One half of the plots were protected with plastic mesh netting (6.4-mm aperture; Internet, Inc. Minneapolis, MN), whereas hard clams in the remaining plots were not covered (control plots). Control and covered plots were arrayed randomly within a 7 × 2 matrix with 5-m spacing between rows and columns. The site was visited on 4 postplanting occasions: July 6, August 14, September 30, and December 22. Quantitative samples using a circular coring device (area = 0.0182 m<sup>2</sup> to a depth of 15 cm) were taken on July 6 (2 cores taken from  $n = 3$  control and  $n = 4$  netted plots) and September 30 (2 cores taken from  $n = 5$  control and netted plots). Clams were sampled using hoes



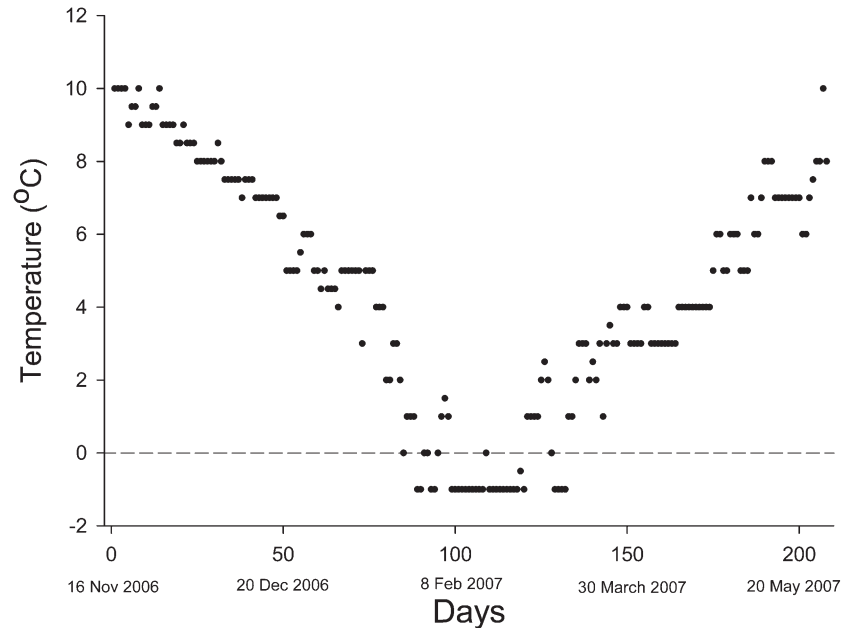


Figure 2. Daily, ambient seawater temperature taken within a 35,000-L tank at the Downeast Institute, Beals, ME, from November 16, 2006 to May 26, 2007.

(sensu Robinson & Rowell 1990) on August 14 and December 22. It is assumed that animals taken in these samples were representative of the population in the plots at the time. On each sampling date, survival was estimated by comparing number of live to dead individuals in each sample, and growth was estimated by measuring 2 linear shell dimensions for each individual. As with cultured individuals of the softshell clam, once hatchery-reared hard clams are placed in sediment, a distinct disturbance line is deposited in the shell that marks individuals uniquely at a size coinciding with their shell length on the planting date (sensu Beal et al. 1999). The length of this disturbance line (initial shell length) and final shell length (greatest anterior–posterior length) were measured as described earlier.

#### Duck Brook Flat, Cutler, ME (June 19 to November 23, 2007)

Cultured hard clam juveniles that had been overwintered at DEI were planted on June 19, 2007, at Duck Brook Flat, Cutler, ME (44°41.18'N; 67°18.66'W) between the mid and lower intertidal zone in circular, plastic horticultural pots (experimental units, 15 cm diameter × 15 cm deep; as described in Beal [2006b]) that had been filled with ambient sediments. Units, arrayed in a matrix with 1-m spacing between rows and columns, were forced into the sediments so only a 1-cm lip was exposed above the sediment. Clams ( $\bar{x}_{SL} \pm 95\% \text{ CI} = 9.3 \pm 0.15 \text{ mm}$ ,  $n = 84$ ) were seeded at 1 of 3 densities per unit: 6, 12, or 24, representing stocking densities of 330, 660, and 1,320 individuals/m<sup>2</sup>, respectively. Five replicates of each density treatment were used, and all experimental units were covered with a piece of 6.4-mm flexible mesh netting (as described earlier) to deter predators. (We were only interested in determining whether hard clams could grow and survive in this region where no wild populations exist.) Units were excavated on November 23, 2007, and the contents of each were washed through a 2-mm sieve. All live, dead, and missing clams were

counted. To assess growth, final shell length of all live clams was measured as described earlier.

#### Statistical Analyses

Data were analyzed using the SAS 9.1 (Statistical Analysis Systems, Cary, NC) statistical package. Statistical significance was determined using a decision rule of  $\alpha = 0.05$  level for all tests, except in the case of *a priori* contrasts (discussed later). Shapiro-Wilk's normality test and Cochran's test of variance homogeneity were conducted on each dependent variable (described later) to test assumptions prior to performing analysis of variance (ANOVA). If violations of either assumption occurred, data were transformed or ranked according to Zar (1999). All data are presented as untransformed means with their corresponding 95% CIs.

#### Nursery Grow-out Trials at Mud Hole Cove, Beals, ME

A single-factor ANOVA was performed on the untransformed mean shell length data. The count data of live clams from the nursery tray experiment could not be transformed to meet the normality assumption; therefore, ANOVA was conducted on the ranks. For both dependent variables, a series of *a priori* contrasts was conducted based on an expectation of food limitation (decreasing growth rate) with increasing stocking density (Bayne et al. 1988) as follows:

1.  $\bar{x}_{2500}$  versus  $\bar{x}_{(5000, 7500, \text{ and } 10,000)}$
2.  $\bar{x}_{5000}$  versus  $\bar{x}_{(7500 \text{ and } 10,000)}$
3.  $\bar{x}_{7500}$  versus  $\bar{x}_{10,000}$

To avoid excessive type I errors, an adjusted alpha ( $\alpha' = 1 - [1 - \alpha]^{1/n}$ ; where  $\alpha = 0.05$  and  $n =$  number of contrasts;  $\alpha' = 0.01695$ ) was used as a decision rule for these contrasts (Winer et al. 1991).

A  $4 \times G$ -test of independence was performed on the size frequency data after organizing into 8 discrete size classes (measured

in millimeters shell length) as follows:  $\leq 5.0$  mm, 5.1–6.0 mm, ... 10.1–11.0 mm,  $\geq 11.1$  mm. The expectation was that the percent frequencies of classes denoting larger shell length would decrease with increasing stocking density. *A priori*, orthogonal contrasts (as noted earlier) were used to investigate this assumption.

**Overwintering Trials at the Downeast Institute**

ANOVA was performed on the ranked percent survival from each of the treatments in which “large” clams were used.

**Field Grow-out Trials at Goose Cove, Trenton, ME**

A 2-way, nested ANOVA (sources of variation include predator exclusion [a = 2, netted vs. control]; time [b = 2, July 6 vs. September 30]; predation  $\times$  time; plot(predation  $\pm$  time) [c = 3, 4, or 5] was conducted on the square root-transformed mean number of hard clam juveniles in quantitative samples and the untransformed mean absolute growth (final shell length – initial shell length). A 4  $\times$  4 G-test of independence was

conducted to determine whether size frequency distribution (independent of netting treatment) varied through time (size measured in millimeters shell length:  $\leq 13$  mm, 13–15 mm, 15–20 mm,  $\geq 20$  mm; sampling dates: July 6, August 14, September 30, December 22). The overall G-statistic was decomposed into 3 orthogonal components (Sokal & Rohlf 1995) to test for seasonal growth.

**Field Grow-out Trials at Duck Brook Flat, Cutler, ME**

A single-factor ANOVA was conducted on the untransformed mean final shell length per experimental unit and the arcsine-transformed mean percent survival per unit to estimate differences in shell growth and survival, respectively, resulting from stocking density. Two *a priori* contrasts were incorporated into the ANOVA linear model for both dependent variables:

1.  $\bar{X}_{330 \text{ m}^{-2}}$  versus  $\bar{X}_{(660 \text{ m}^{-2} + 1320 \text{ m}^{-2})}$
2.  $\bar{X}_{660 \text{ m}^{-2}}$  versus  $\bar{X}_{1320 \text{ m}^{-2}}$

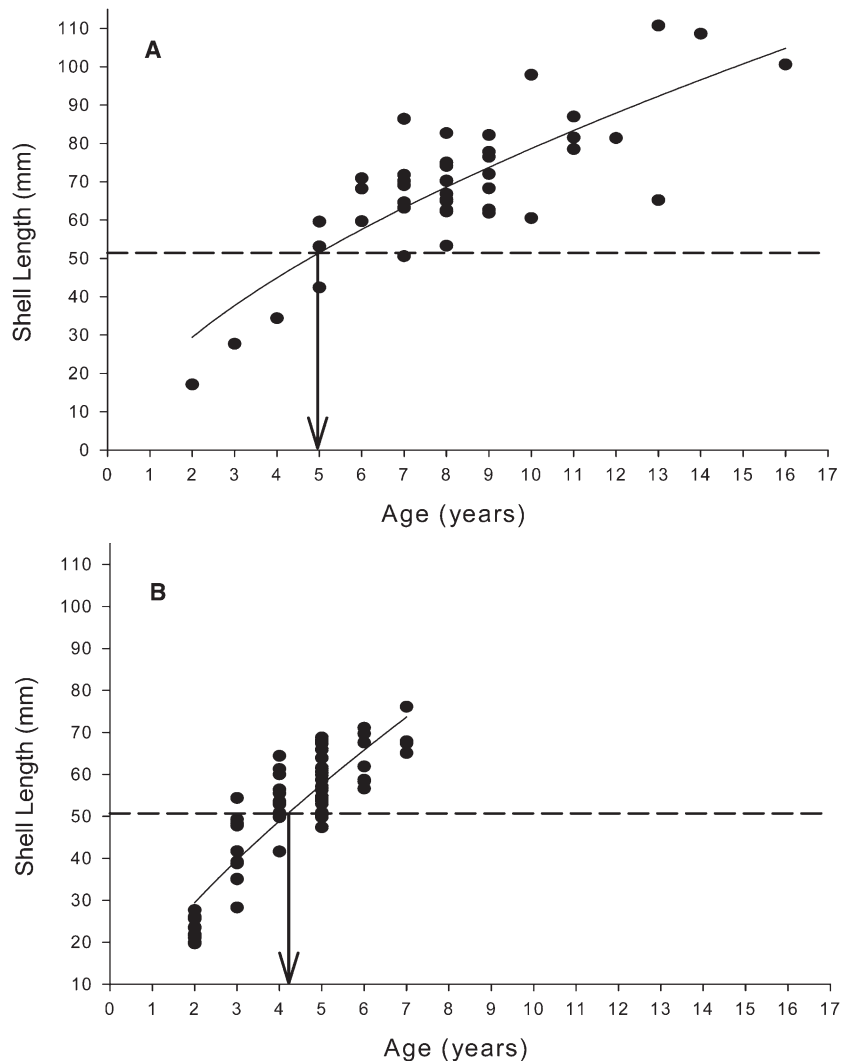


Figure 3. Age-length relationship for 2 growth morphs sampled on December 7, 2005, at Goose Cove, Trenton, ME. Analysis of covariance determined that the log-transformed lines were significantly different ( $P < 0.0001$ ). (A) Power exponential equation for the slower-growing individuals is  $Y = 13.99 \times X^{0.757}$ ;  $r^2 = 0.759$ ;  $F = 132.8$ ;  $df = 1, 42$ ;  $P < 0.0001$ ;  $n = 44$ ; where Y is length and X is age (in years). (B) Equation for the faster growing individuals is  $Y = 14.068 \times 0.881^X$ ;  $r^2 = 0.829$ ;  $F = 314.02$ ;  $df = 1, 65$ ;  $P < 0.0001$ ;  $n = 67$ . Arrows indicate approximate time in years to reach a commercial shell length of 50.8 mm (2 inches).

TABLE 1.

**Analysis of variance on the mean shell length of *M. mercenaria* from the field experiment conducted at Mud Hole Cove, Great Wass Island, Beals, ME, from July 5–6 to November 16, 2006.**

Source of Variation	df	SS	MS	F Value	Pr > F
Intraspecific density	3	6.48	2.16	17.63	<0.0001
2,500 vs. rest	1	4.88	4.88	39.85	<0.0001
5,000 vs. rest	1	1.16	1.16	9.48	0.0029
7,500 vs. 10,000	1	0.44	0.44	3.57	0.0625
Error	76	9.32	0.12		
Total	79	15.80			

The 4 stocking densities included 2500, 5000, 7500, and 10,000 per tray (1.08 m<sup>2</sup>;  $n = 20$ ). Single degree-of-freedom contrasts used a decision rule ( $\alpha'$ ) = 0.01695. MS = mean square; SS = sums of squares; PR > F = probability F'-value.

An adjusted  $\alpha'$  of 0.02532 was used as a decision rule for these contrasts.

## RESULTS

### Wild Clam Growth in Trenton, ME

A linear relationship existed between the number of internal versus external lines:  $Y_{(\text{internal})} = -0.807 + 1.119 X_{(\text{external})}$  ( $r^2 = 0.957$ ;  $P < 0.0001$ ;  $n = 16$ ) suggesting nearly a 1:1 relationship. Because internal lines are thought to be annual markers (Henry & Cerrato 2007), especially near the latitude where they were collected (LeBlanc et al. 2005), external lines were used to age the remaining individuals. In addition, we noticed that the inner surface of the valves of 44 of the 111 animals had a dark (purple) coloration near the ventral margin in the area of the siphons, and that these clams appeared to have more external lines for a given length than clams without the purple coloration. To test whether these clams were growing more slowly than those without the inner surface purple marking, we performed a regression analysis

to determine whether the log-transformed age-length relationship yielded similar slopes ( $F = 2.36$ ;  $df = 1, 107$ ;  $P = 0.1275$ ). Analysis of covariance demonstrated that the 2 lines were significantly different ( $F = 31.78$ ;  $df = 1, 108$ ;  $P < 0.0001$ ), suggesting that 2 growth morphs occurred at the same location (Fig. 3).

### Field Nursery Grow-out Trials (July 5 to November 16, 2006)

No dead animals or empty valves were recovered on November 16, 2006, in any of the 80 trays stocked with cultured *M. mercenaria*. Stocking density had a highly significant effect on mean shell length of cultured *M. mercenaria* ( $P < 0.0001$ ; Table 1, Fig. 4). Mean shell length for each density (2,500, 5,000, 7,500, and 10,000) was  $8.4 \pm 0.13$  mm,  $8.0 \pm 0.12$  mm,  $7.9 \pm 0.18$  mm, and  $7.6 \pm 0.218$  mm, respectively. Orthogonal contrasts demonstrated that mean shell length of hard clams stocked in trays at a density of 2500 individuals was significantly larger than the mean from animals pooled over the other 3 densities ( $P < 0.0001$ ; Table 1). Similarly, animals held at 5,000 per tray were significantly larger than animals at the 2 higher densities pooled together ( $P = 0.0029$ ; Table 1); however, mean shell length of clams at the 2 highest densities was not significantly different ( $P = 0.0625$ ; Table 1). A trend analysis indicated that the relationship between mean shell length and stocking density was negative and linear ( $P < 0.001$ ). No significant deviations from linearity were detected ( $P > 0.25$ ).

Mean number of juveniles of *M. mercenaria* per 14-g sample increased linearly with stocking density ( $P < 0.0001$ ; Fig. 5). Mean counts across each stocking density (2,500, 5,000, 7,500, and 10,000) were  $65.6 \pm 5.28$  clams,  $78.9 \pm 3.79$  clams,  $86.2 \pm 7.98$  clams, and  $93.6 \pm 5.94$  clams, respectively. ANOVA on the ranked count data demonstrated a significant effect resulting from stocking density ( $P < 0.001$ ; Table 2). The comparison of means of the 2 highest densities was the only contrast that was not statistically significant ( $P < 0.026$ ).

Size frequency distribution of cultured *M. mercenaria* varied significantly across stocking density treatments ( $P < 0.0001$ ;

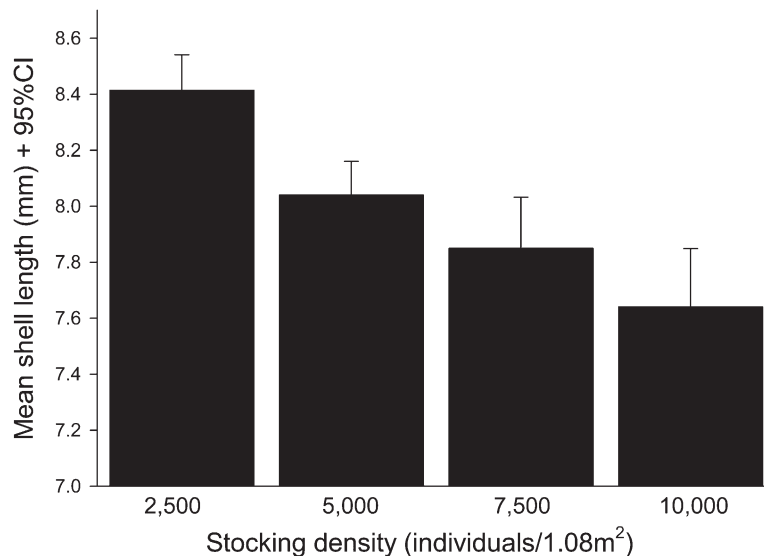


Figure 4. Relationship between stocking density and mean shell length of hard clams held in floating trays (1.08 m<sup>2</sup>) at Mud Hole Cove, Great Wass Island, Beals, ME, from July 5–6 to November 16, 2006. ANOVA (Table 1) revealed a significant effect on mean shell length resulting from stocking density. A trend analysis indicated a negative linear relationship between dependent and independent variables ( $n = 20$ ).

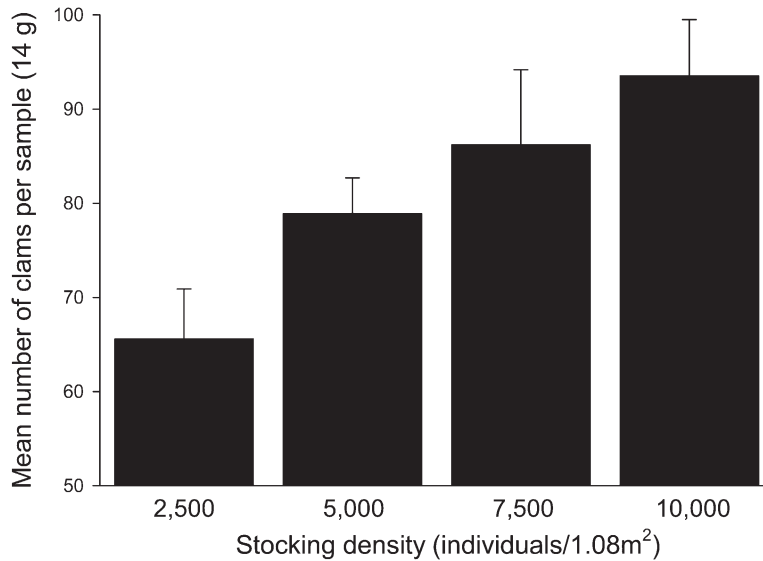


Figure 5. Mean number (+95% CI) of hard clams in 14-g samples from floating trays at Mud Hole Cove, Great Wass Island, Beals, ME, from July 5–6 to November 16, 2006, as a function of initial stocking density. ANOVA on the ranked data (Table 2) indicated that counts of hard clams per tray increased significantly with increasing stocking density ( $n = 20$ ).

Table 3; Fig. 6). All 3 orthogonal contrasts were significant ( $P < 0.005$ ), and each indicated a greater proportion of individuals occurred in the larger size classes in the smallest density of the comparison. In general, the proportion of smaller shell length increased with increasing stocking density. The distribution associated with clams stocked at 2,500 and 10,000 individuals per tray was skewed to the left and right, respectively, whereas the distribution for the 2 middle stocking densities were normally distributed ( $P > 0.10$ ).

*Overwintering Trials at the Downeast Institute (November 16, 2006 to May 13, 2007)*

Overall mean percent survival for the “large” clams for the 177-day experiment was  $99.4 \pm 0.28\%$  ( $n = 42$ ). No significant effect resulting from mass treatments was observed ( $P = 0.9842$ ). “Small” clam survival was  $99.7 \pm 0.24\%$  ( $n = 16$ ). No

significant shell growth occurred for any size clam or in any mass treatment.

*Field Grow-out Trials*

**Goose Cove, Trenton, ME (May 20 to December 22, 2007)**

Quantitative samples taken on July 6 and September 30 2007 (47 and 133 days after seeding plots), demonstrated no significant hard clam losses between the two dates ( $0_{\text{July}} = 17.5 \pm 6.6$  [ $n = 7$ ] vs.  $0_{\text{September}} = 14.6 \pm 2.1$  [ $n = 10$ ] individuals per core), and no significant difference in mean number between netted and control plots ( $0_{\text{Netting}} = 16.3 \pm 4.4$  [ $n = 9$ ] vs.  $0_{\text{Control}} = 15.2 \pm 3.8$  [ $n = 8$ ] individuals per core; Table 4; Fig. 7). Mean absolute growth from May to December was  $9.3 \pm 0.3$  mm and final mean shell length was  $17.9 \pm 0.367$  ( $n = 244$ ). No significant effect resulting from presence of netting was detected on mean absolute growth ( $P = 0.721$ ). Size frequency distribution varied significantly through time (Fig. 8), and the G-test of independence

TABLE 2.

**Analysis of variance on the ranked mean number of cultured juveniles of *M. mercenaria* from 14-g samples per tray (1.08 m<sup>2</sup>) from the nursery field experiment conducted at Mud Hole Cove, Great Wass Island, Beals, ME from July 5–6 to November 16, 2006.**

Source of Variation	df	SS	MS	F Value	Pr > F
Density	3	18,204.78	6,068.26	18.90	<0.0001
2,500 vs. rest	1	13,680.60	13,680.60	42.61	<0.0001
5,000 vs. rest	1	2,866.52	2,866.52	8.93	0.0038
7,500 vs. 10,000	1	1,657.66	1,657.66	5.16	0.0259
Error	76	24,402.23	321.08		
Total	79	42,607.00			

The 4 stocking densities included 2,500, 5,000, 7,500, and 10,000 per tray (1.08 m<sup>2</sup>;  $n = 20$ ). Single degree-of-freedom contrasts used a decision rule ( $\alpha'$ ) = 0.01695.

TABLE 3.

**Analysis of size frequencies of *M. mercenaria* (4 × 8 G-test of independence; stocking density × size class) from the field experiment conducted at Mud Hole Cove, Great Wass Island, Beals, ME from July 5–6 to November 16, 2006.**

Analysis	df	G Value	P Value
Overall analysis of frequencies	21	334.50	<0.0001
(2,500 versus rest)	7	223.05	<0.0001
(5,000 versus rest)	7	75.52	<0.0001
(7,500 versus 10,000)	7	28.51	0.0002

The 4 stocking densities of cultured clams included 2,500, 5,000, 7,500, and 10,000 per tray (1.08 m<sup>2</sup>;  $n = 20$ ). (See text for definition of size classes.) A decision rule ( $\alpha'$ ) for each orthogonal contrast = 0.01695.



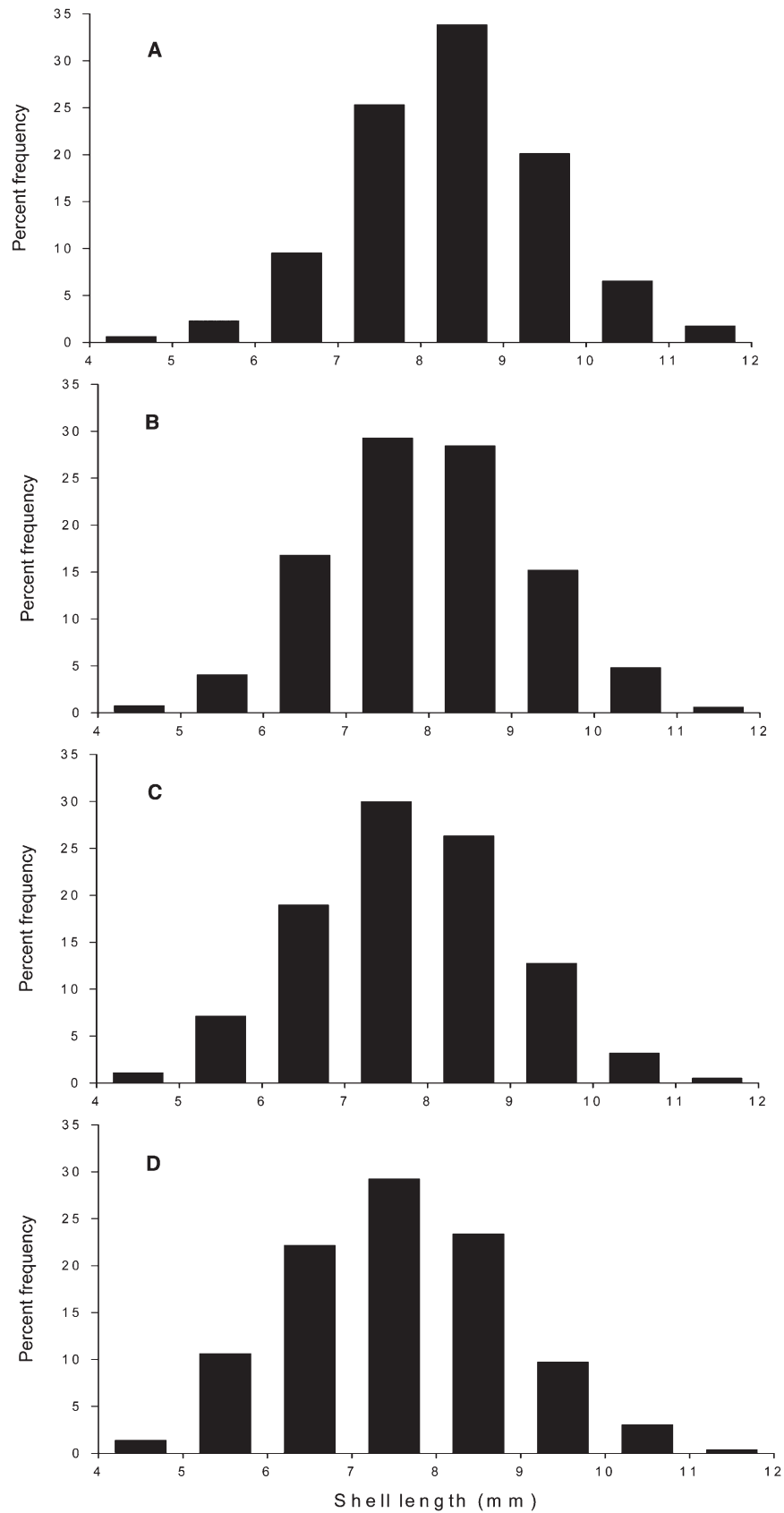


Figure 6. (A–D) Size–frequency distribution of hard clams held in floating trays from July 5–6 to November 16, 2006, from each of twenty 14-g samples from each of 4 stocking densities. Number of clams measured for the 2,500 (A), 5,000 (B), 7,500 (C), and 10,000 (D) density treatments was 1,312, 1,578, 1,724, and 1,871, respectively.

TABLE 4.

Analysis of variance on the square root-transformed mean number of juveniles of *M. mercenaria* per core (0.0182 m<sup>2</sup>) taken on July 6 and September 30, 2007, at Goose Cove, Trenton, ME.

Source of Variation	df	SS	MS	F Value	Pr > F
Netting (present vs. absent)	1	0.115	0.115	0.12	0.7318
Sampling date (July vs. September)	1	0.678	0.678	0.72	0.4109
Netting × sampling date	1	0.297	0.297	0.32	0.5832
Plot (netting × date)	13	12.209	0.939	0.84	0.6224
Error	17	19.084	1.123		
Total	33	32.383			

Seed ( $8.2 \pm 0.15$  mm; shell length range = 4.8–12.0 mm,  $n = 100$ ) was added to netted and control plots at an approximate density of 540/m<sup>2</sup> on May 20, 2007. (See Materials and Methods for number of samples taken from plots on both dates.)

(Table 5) indicated changes in the distribution from September to December, suggesting that some shell growth did occur during that period. Using mean shell length (Fig. 9), it appears that 60% of shell growth between May and December occurred before mid August, and that approximately 15% occurred between September and December.

#### Duck Brook Flat, Cutler, ME (June 19 to November 23, 2007)

A total of 204 of the 210 animals added to experimental units in June 2007 were recovered alive. All hard clams in each experimental unit from the lowest and highest density treatment survived. Overall survival was  $97.2 \pm 3.8\%$  ( $n = 15$ ). Final mean shell length was  $14.3 \pm 0.3$  mm ( $n = 15$ ), and effects resulting from stocking density on final shell length were not statistically significant ( $P = 0.1043$ ).

## DISCUSSION

Results presented here are the first ever to be reported for northern hard clam growth and survival in east coastal Maine.

Hard clams are distributed intertidally in soft sediments along the Maine coast from the border with New Hampshire to Frenchman's Bay, a linear distance of approximately 250 km. Commercial populations exist near the low tide mark in several flats in the vicinity of Goose Cove in Trenton (near Mt. Desert Island, Fig. 1); however, no commercial activities exist east of this area, and we are unaware of any published or anecdotal reports of populations of this bivalve occurring in eastern Hancock County or anywhere along the coast of Washington County (Fig. 1). Because the hard clam population in Frenchman's Bay is self-sustaining, we presume that at least 1 of 2 abiotic factors operate to limit hard clam distributions from far eastern Maine. First, the net flow of seawater along the Maine coast is southwestward (Pettigrew et al. 2005). Strongest flows, resulting primarily from tidal currents associated with the Eastern Maine Coastal Current (Bay of Fundy to Penobscot Bay), can reach velocities up to 50 cm/sec near the surface (Brooks & Townsend 1989). Larvae of hard clams produced in and around Frenchman's Bay likely would be transported to the south and west, in the opposite direction from east coastal Maine. Second, although the temperature at which *M. mercenaria* spawns differs throughout its geographical range, water temperatures between 18–26°C generally trigger spawning (Eversole 2001). In addition, normal larval development proceeds at seawater temperatures between 18–30°C (Loosanoff & Davis 1963). Because summer seawater temperatures more than 15°C are uncommon in far eastern Maine (Townsend et al. 2005), it is unlikely that *Mercenaria* would be reproductively successful in this region.

#### Growth of Wild *Mercenaria*

We observed 2 growth morphs (sensu Vadas et al. 2002) collected from the lower intertidal of Goose Cove, Trenton, ME. Regardless of size, animals with a purple coloration near the anterior region on the internal portion of each valve near the pallial sinus grew significantly slower than animals without this marking. There were no differences in the external shell morphology to distinguish these 2 groups other than the width between annual growth lines, which was narrower in the slower

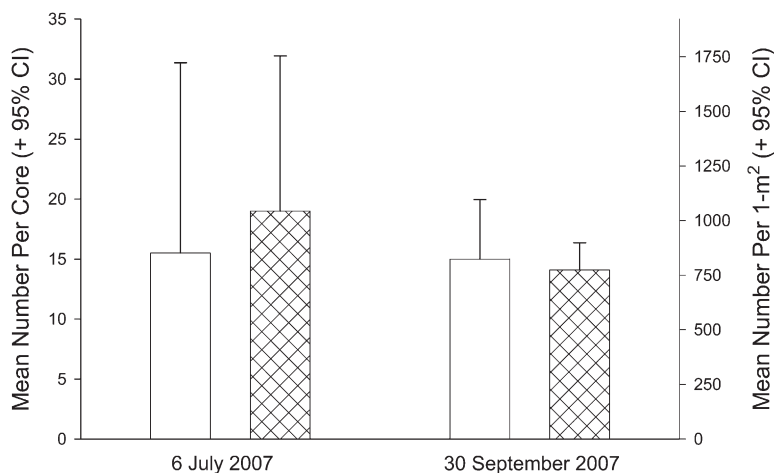


Figure 7. Mean number of hard clam juveniles per core and per square meter sampled from control (open bars) and netted (cross-hatched bars) plots on July 6 and September 30, 2007, at Goose Cove, Trenton, ME. Animals ( $8.2 \pm 0.15$  mm shell length) were seeded into plots at a density of 540/m<sup>2</sup> on May 20, 2007. (See Materials and Methods for sample sizes.)

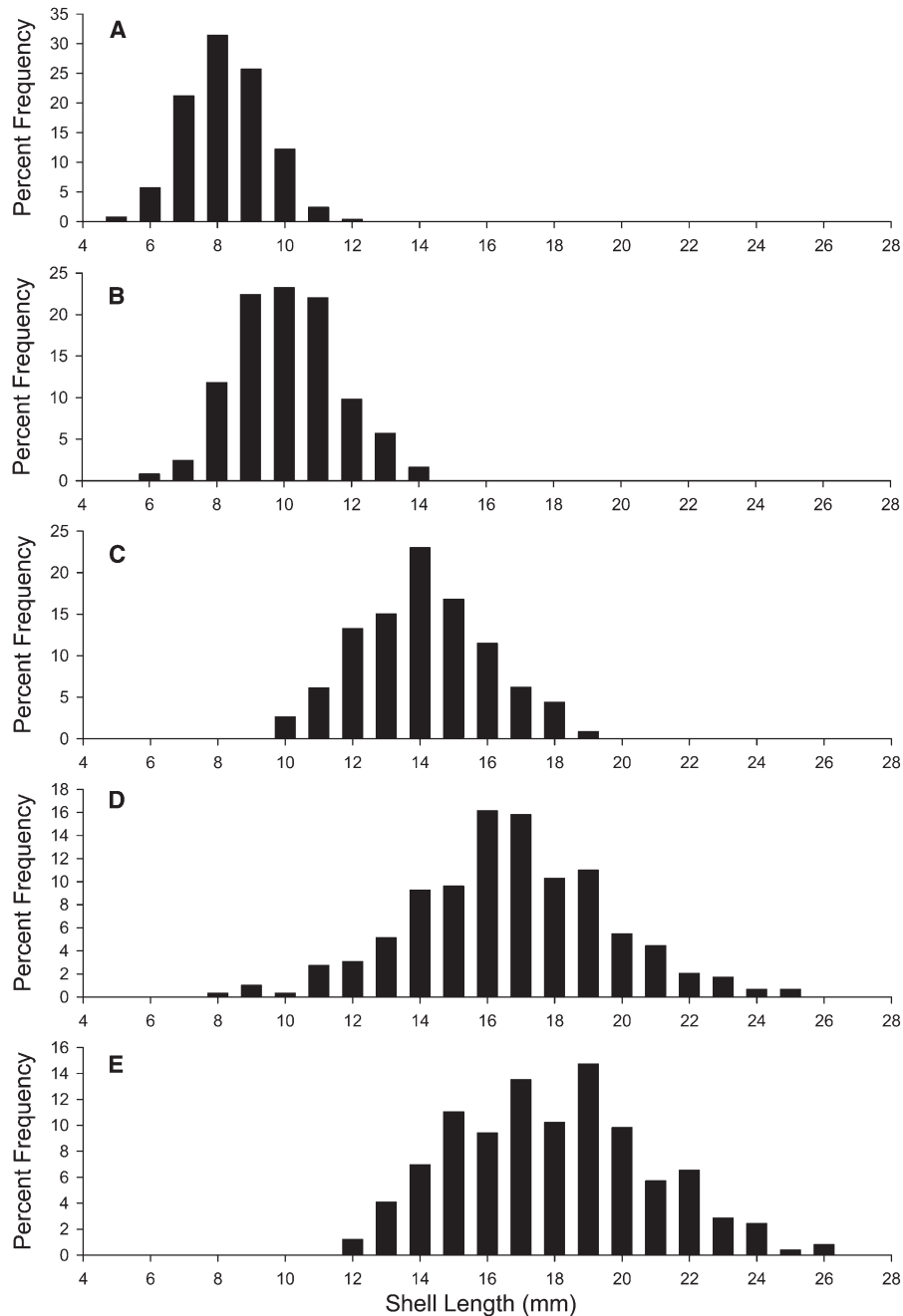


Figure 8. Size frequency distribution of cultured hard clams at Goose Cove, Trenton, ME, during seasonal sampling in 2007. (A) May 20: mean shell length =  $8.2 \pm 0.15$  mm,  $n = 100$ . (B) July 6:  $n = 245$ . (C) August 14:  $n = 113$ . (D) September 30:  $n = 291$ . (E) December 22: mean shell length =  $17.9 \pm 0.3$  mm,  $n = 244$ . Juveniles were seeded into protected (netted) and control plots ( $22.2 \text{ m}^2$ ) at a density of  $540/\text{m}^2$ . No significant difference in mean shell length was observed on any date between the 2 plot types ( $P > 0.40$ ). A  $4 \times 4$  G-test of independence (size  $\times$  sampling date) was statistically significant (Table 5).

growing morph. Because these animals were not sampled discretely, but collected by commercial raking, we do not know the proximate cause for the 2 growth morphs. Possible explanations may include density-dependent interactions that could suppress growth (e.g., Peterson 1982, Ólafsson 1986), differential settlement or recruitment from 2 distinct (genetic) populations, or some postsettlement process such as gape-limited predation (sensu Urban 2007) that has the potential to select for both fast- and slow-growth strategies.

Growth rate of both morphs slowed with increasing shell length, and was similar to that observed for more southern populations in Maine. For example, Ansell (1968) reported that “best” growth of hard clams from 11 southern Maine locations sampled by Gustafson (1955) was 4.75 y to reach a shell length of 50.8 mm. This rate is intermediate between the slow and fast morph at Goose Cove (Fig. 3). In addition, Gustafson (1955) reported that hard clams grew seasonally from March to November, with the fastest daily increment occurring between

TABLE 5.

**Analysis of size frequencies of juveniles of *M. mercenaria* ( $4 \times 4$  G-test of independence; sampling date  $\times$  size class) from the field experiment conducted at Goose Cove, Trenton, ME, from May 20 to December 22, 2007.**

Analysis	df	G Value	P Value
Overall analysis of frequencies	9	782.26	<0.0001
July/August vs. September/December	3	579.21	<0.0001
July vs. August	3	185.18	<0.0001
September vs/ December	3	17.87	0.0005

Animals were seeded into 22.2-m<sup>2</sup> plots with and without protective netting at a density of 540/m<sup>2</sup>. A decision rule ( $\alpha'$ ) for each orthogonal contrast = 0.01695.

June and September. No other published reports on hard clam growth from Maine waters exist, but growth rates are significantly slower in populations east of Maine, where commercial harvests occur in the Canadian Maritimes. *Mercenaria* are harvested in St. Mary's Bay, Nova Scotia, where summer water temperatures exceed 20°C (Landry & Sephton 1996). In that location, quahogs reach commercial shell length in 7 y (LeBlanc et al. 2005). In Prince Edward Island, near the northern limit of hard clams, Landry et al. (1993) reported that it can take up to 13 y to reach 50 mm, although Kerswill (1949) showed that quahogs near the mouth of the Biddeford River, near Port Hill Wharf, reach a 50-mm shell length in an average of 7 y.

#### Nursery Grow-out and Overwintering Trials Using Cultured Seed

Growth rate was density dependent in the floating nursery trays from early July to mid November 2006, with final length a negative, linear function of stocking density (Fig. 4). Fastest growth occurred among clams held at 2500 per tray (2315/m<sup>2</sup>).

Mean shell length was  $8.4 \pm 0.13$  mm (range, 4.1–13.9 mm), and 9% of the animals attained sizes larger than 10 mm. Conversely, only 3.7% of the animals held at 10,000 per tray (9260/m<sup>2</sup>) reached sizes larger than 10 mm. Floating nursery trays were used in these trials, instead of upwellers, FLUPSYs, or other configurations such as raceways (see Flimlin 2000, Pfeiffer & Rusch 2007), because they have proved the most successful strategy for nursery grow-out of cultured softshell clam (*Mya arenaria*) seed in this geographical region for more than 20 y (Beal 2005). Although growth rates of *M. mercenaria* seed in eastern Maine at the nursery site were extremely slow compared with rates in coastal regions south of Maine (e.g., Eldridge et al. 1976, Hadley & Manzi 1984, Castagna 2001), final mean shell length was sufficiently large for transplanting to field grow-out sites, especially if protected with netting, based on culture programs elsewhere (Malinowski 1986, Kraeuter & Castagna 1989, Peterson et al. 1995).

Transplanting hard clam seed to field grow-out sites typically occurs after seed has reached its maximum size in a nursery. In eastern Maine, growth of softshell clams ceases during late October/early November (Beal 2006a), and it appears that hard clams have similar seasonal growth patterns (described later). Transplanting cultured softshell clam (*M. arenaria*) seed to intertidal flats during the fall is not advised because of the high risk of mortality over the winter caused by ice scour and rafting of the top few centimeters of sediment (Beal et al. 1995). Because postnursery hard clam seed would be similar in size to cultured *Mya* seed, transplanting to intertidal flats in the fall would expose cultured *Mercenaria* juveniles to the same environmental conditions. We presume overwinter mortalities would be high in eastern Maine, at least in years when ice is present. In the Canadian Maritimes, field mortalities of hard clam seed exceeding 20% for native and 50% for the notata variety (Humphrey & Walker 1982) during the first winter have been described (Witherspoon 1984, MacNair 2003; Bricelj et al. 2005). Our successful overwintering trials (November 2006 to May 2007) at the DEI build upon similar technology used for nearly 2 decades to

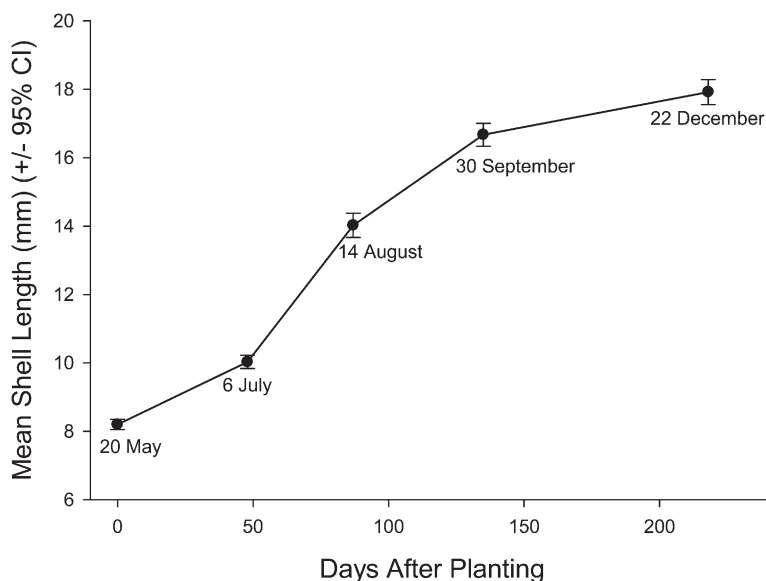


Figure 9. Mean shell length ( $\pm 95\%$  CI) of cultured hard clams at Goose Cove, Trenton, ME, at the beginning of the field experiment (May 20, 2007) and on 4 subsequent sampling dates. See Figure 8 for number of animals measured on each sampling date.

overwinter softshell clam seed for spring plantings (Beal et al. 1995). We observed overwinter (177 days) survival rates exceeding 99%, and are unaware of any published reports of similar rates for cultured hard clam seed (< 10 mm shell length).

Pernet et al. (2006) examined how decreasing temperatures (24°C to 0°C) affect membrane lipids in 2 strains (wild vs. notata) of cultured hard clam juveniles in the Gulf of St. Lawrence, near Neguac, New Brunswick. Wild clams exhibited lower oxygen consumption rates and a lower heterozygote deficiency than the selectively bred hard clams. Marked deviations from Hardy-Weinberg equilibrium at several loci were believed to impose additional stress, resulting in higher overwinter mortalities for the notata compared with the wild strain. Working at the same field site, Gionet et al. (2008) discovered that approximately 50% of notata strain juveniles died during the winter compared with approximately 10% of the wild (i.e., native) strain. This disparity in survival paralleled each strain's ability to stock lipids. For example, wild individuals had higher concentrations of lipids and glucose than notata individuals, and they inferred that elevated concentrations of glucose may act as a cryoprotectant by helping to reduce the freezing point of intercellular fluids and tissues.

Overwinter mortality represents a significant problem for mid-Atlantic and Northeast aquaculturists (Greene & Becker 1977, Krauter & Castagna 1984, Krauter & Ford 1997, Fegley 2001, Zarnoch & Schreiberman 2008), who report losses of hard clam seed in excess of 25%. Zarnoch and Schreiberman (2008) observed that lipid content played a minimal role in the physiological energetics during the winter. Instead, they showed a relationship between decreasing carbohydrate reserves and increased mortality rates. Hard clams apparently reduce their metabolism to  $\leq 5\%$  of the normal metabolic rate at temperatures less than 5°C, and this strategy enables them to conserve energy reserves; however, as seawater temperatures increase through the spring, they depend upon endogenous energy reserves from phytoplankton to support increased metabolic activity. If, after an extended cold winter, spring blooms are late or relatively unproductive, losses of nearly 1% per day occur. Zarnoch and Schreiberman (2008) referred to this phenomenon as "winter-spring" mortality. The excellent survival of cultured hard clam seed held at high densities in flow-through conditions over the winter at the DEI (Beals, ME) has been replicated twice, during the winters of 2007–2008 and 2008–2009. Spring plantings have coincided with excellent survival at intertidal field grow-out sites (described later). Whether quahog seed originating from Goose Cove broodstock are genetically better adapted to temperature stress by using less energy stores and/or the particular overwintering technique produces viable, healthy individuals for spring plantings remains to be tested.

#### Field Grow-out Trials

Growth of hard clam seed at Goose Cove was highly seasonal, with greatest incremental increases in shell growth occurring between early July and late September (Fig. 9). Similar patterns were observed at intertidal sites east of Goose Cove with cultured softshell clam juveniles (Beal et al. 2001). Gustafson (1955) followed the growth of wild hard clam juveniles (initial size, 23 mm shell length; no stocking density given) in intertidal plots located near Freeport, ME (43°48.69'N; 70°06.54'W) for 12 months beginning June 1952. Similar to results from Goose Cove, shell length at the southern Maine site increased nearly

linearly from June through October, when 83% of the annual growth occurred, but then slowed down and leveled off until the beginning of December. No appreciable increase in shell length was observed until the following April. Clams added an average of 16.6 mm of new shell during the year, of which 14.5 mm was added between June and December.

Survival of hard clams at Goose Cove, measured quantitatively on July 6 and September 30, 2007, by taking benthic cores in the field plots, was high, with minimal losses resulting from epibenthic predators (Table 4). Hard clams were seeded at a density of approximately 540/m<sup>2</sup> in May 2007, and density estimates in September (mean, 802 individuals/m<sup>2</sup>, or 14.6/core) were significantly higher than what one would have expected if zero mortality had occurred (one-sample *t*-test;  $T = 5.73$ ,  $df = 9$ ,  $P < 0.001$ ). Presumably, some postseeding process resulted in clumping of individuals. Another explanation could be that wild quahog juveniles were confused for cultured juveniles. However, hatchery seed have a conspicuous disturbance line that coincides with size at the time of planting, so it was not difficult to separate wild from cultured juveniles. No matter the mechanism, the very high survival was observed in both netted and control plots. Two of us initiated another field experiment in May 2008 at the same site and tidal height using similar-size hard clam seed that had been overwintered (as described earlier), and observed similar survival rates in both netted and control plots by December 2008 (Beal and Porada, unpublished).

Field trials in Cutler (far eastern Maine) from mid June to late November demonstrated that quahogs can grow within the intertidal in this geographical region, but that shell growth was slow. Animals increased in size by only 5 mm during that period. A similar field trial using cultured hard clam seed was conducted at the same site and tidal height from early June to mid-November 2008. Animals (initial shell length, 6.8 mm) added an average of only  $3.4 \pm 0.7$  mm ( $n = 15$ ) of new shell during this interval (Beal, unpublished).

Overall, these results are encouraging regarding future development of hard clam farms in eastern Maine, and our overwintering results may be generalizable to other populations of cultured seed from the mid Atlantic to the Canadian Maritimes. Broodstock from Goose Cove can be used to produce cultured juveniles that, to date, survive well for the first growing season when seeded into field plots in the spring. Farming quahogs in eastern Maine has the potential to diversify a sagging shellfish industry that has seen declining landings of softshell clams, sea scallops (*Placopecten magellanicus*), ocean quahogs (*Arctica islandica*), and sea urchins (*Strongylocentrotus droebachiensis*) during the past decade. The first stages in developing these activities are encouraging, but long-term success will depend on good survival to a size that will have to be developed for the smallest animals acceptable to the consumer in conjunction with a marketing strategy that capitalizes on the pristine nature of the grow-out locations. Additional field trials to examine other grow-out locations, and alternative methods to enhance growth rates are needed.

#### ACKNOWLEDGMENTS

This work was funded by a seed grant from the Maine Technology Institute (SG2679) and the University of Maine at Machias. C. Jourdet, K. Pepperman, E. Darga, and A. Zsak



assisted in the culture portion of this work, and C. Jourdet and K. Pepperman provided field assistance. We thank C. Zarnoch, W. Walton, and J. Kraeuter for discussions about overwinter-

ing hard clam seed. We appreciate the unrestricted access to intertidal flats at Goose Cove thanks to the Town of Trenton, and at Duck Brook Cove in Cutler thanks to D. Monroe.

## LITERATURE CITED

- Anonymous. 2007. Gulf of Maine Ocean Observing System. Environmental data from Jonesport buoy. <http://www.gomoos.org/gnd/>.
- Ansell, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographical range. *J. Cons. Perm. Int. Explor. Mer* 31:364–409.
- Bayne, B. L., A. J. S. Hawkins & E. Navarro. 1988. Feeding and digestion in suspension-feeding bivalve mollusks: the relevance of physiological compensations. *Am. Zool.* 28:147–159.
- Beal, B. F. 2005. Softshell clam, *Mya arenaria*, mariculture in Maine, USA: opportunities and challenges. *Bull. Aqua. Assoc. Can.* 9:41–44.
- Beal, B. F. 2006a. Biotic and abiotic factors influencing growth and survival of wild and cultured individuals of the softshell clam (*Mya arenaria* L.) in eastern Maine. *J. Shellfish Res.* 26:461–474.
- Beal, B. F. 2006b. Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the soft-shell clam, *Mya arenaria* L., at several spatial scales. *J. Exp. Mar. Biol. Ecol.* 336:1–17.
- Beal, B. F., R. C. Bayer, M. G. Kraus & S. R. Chapman. 1999. A unique shell marker of juvenile, hatchery-reared individuals of the softshell clam, *Mya arenaria* L. *Fish. Bull. (Wash. D. C.)* 97:380–386.
- Beal, B. F., C. Lithgow, D. Shaw, S. Renshaw & D. Ouellette. 1995. Overwintering hatchery-reared individuals of the soft-shell clam, *Mya arenaria* L.: a field test of site, clam size, and intraspecific density. *Aquaculture* 130:145–158.
- Beal, B. F., M. R. Parker & K. W. Vencile. 2001. Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the soft-shell clam, *Mya arenaria* L., in Maine, USA. *J. Exp. Mar. Biol. Ecol.* 264:133–169.
- Bricelj, M. V., C. Ouellette, M. Anderson, N. T. Brun, F. Pernet, N. W. Ross & T. Landry. 2005. Physiological and biochemical responses of juvenile quahogs, *Mercenaria mercenaria*, to low temperatures: potential for mitigation of overwintering mortalities. *Can. Tech. Rep. Fish. Aqua. Sci.* 2739: vii + 44 p.
- Brooks, D. A. & D. W. Townsend. 1989. Variability of the coastal current and nutrient pathways in the eastern Gulf of Maine. *J. Mar. Res.* 47:303–321.
- Castagna, M. 2001. Aquaculture of the hard clam, *Mercenaria mercenaria*. In: J. N. Kraeuter & M. Castagna, editors. *Biology of the hard clam*. New York: Elsevier. pp. 675–700.
- Congleton, W. R., Jr., T. Vassiliev, R. C. Bayer, B. R. Pearce, J. Jacques & C. Gilman. 2006. Trends in Maine softshell clam landings. *J. Shellfish Res.* 25:475–480.
- Dillon, R. T., Jr. & J. J. Manzi. 1987. Hard clam, *Mercenaria mercenaria*, brood stocks: genetic drift and loss of rare alleles without reduction in heterozygosity. *Aquaculture* 60:99–105.
- Dillon, R. T., Jr. & J. J. Manzi. 1992. Population genetics of the quahog, *Mercenaria mercenaria*, at the northern limit of its range. *Can. J. Fish. Aquat. Sci.* 49:2574–2578.
- Dow, R. L. & D. E. Wallace. 1951. A method of reducing winter mortalities of quahogs (*Venus mercenaria*) in Maine waters. *Research Bulletin no. 4*. Augusta, ME: Maine Department of Sea Shore Fisheries. 32 pp.
- Dow, R. L. & D. E. Wallace. 1955. Quahog management in Maine. March 29. Augusta, ME: Maine Department of Sea Shore Fisheries. 2 pp.
- Eldridge, P. J., W. Waltz, R. C. Gracy & H. H. Hunt. 1976. Growth and mortality of hatchery seed clams, *Mercenaria mercenaria*, in protected trays in waters of South Carolina. *Proc. Natl. Shellfish. Assoc.* 66:13–20.
- Eversole, A. G. 2001. Reproduction in *Mercenaria mercenaria*. In: J. N. Kraeuter & M. Castagna, editors. *Biology of the hard clam*. New York: Elsevier. pp. 221–260.
- Fegley, S. R. 2001. Demography and dynamics of quahog populations. In: J. N. Kraeuter & M. Castagna, editors. *Biology of the hard clam*. New York: Elsevier. pp. 383–422.
- Flimlin, G. 2000. Nursery and growout methods for aquacultured shellfish. U.S. Dept. Agriculture, Northeast Regional Aquaculture Center, Univ. Massachusetts, Dartmouth. NRAC Publication no. 00-002, 15 pp.
- Gionet, C., E. Mayrand & T. Landry. 2008. The effect of energy reserves and cryoprotectants on overwintering mortality in *Mercenaria mercenaria* notata (Say 1822) at two tidal levels. *Aquacult. Int.* DOI 10.1005/s10499-008-9229-z 17 p.
- Glude, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. *Trans. Am. Fish. Soc.* 84:13–26.
- Greene, G. T. & D. S. Becker. 1977. Winterkill of hard clams in Great South Bay, NY, 1976–1977. Special report 9(77-5). Stony Brook, NY: Marine Science Research Center, State University of New York. 23 pp.
- Grizzle, R. E. & R. A. Lutz. 1988. Descriptions of macroscopic banding patterns in sectioned polished shells of *Mercenaria mercenaria* from southern New Jersey. *J. Shellfish Res.* 7:367–370.
- Grosholz, E. D. & G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biol. Conserv.* 78:59–66.
- Gustafson, A. H. 1955. Growth studies in the quahog, *Venus mercenaria*. *Proc. Natl. Shellfish Assoc.* 45:140–150.
- Hadley, N. H. & J. J. Manzi. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. *Aquaculture* 36:369–378.
- Henry, K. M. & R. M. Cerrato. 2007. The annual macroscopic growth pattern of the northern quahog [=hard clam, *Mercenaria mercenaria* (L.)], in Narragansett Bay, Rhode Island. *J. Shellfish Res.* 26:985–993.
- Humphrey, C. M. & R. L. Walker. 1982. The occurrence of *Mercenaria mercenaria* form notata in Georgia and South Carolina: calculation of phenotypic and genotypic frequencies. *Malacologia* 23:75–79.
- Ingersoll, E. 1887. The oyster, scallop, quahog, mussel, and abalone industries. In: G. B. Goode, editor. *The fisheries and fishery industries of the United States*. Section II. Washington, DC: U.S. Government Printing Office. pp. 507–626.
- Kerswill, C. J. 1949. Effects of water circulation on the growth of quahaugs and oysters. *J. Fish. Res. Bd. Can.* 7:545–551.
- Kraeuter, J. N. & M. Castagna. 1984. Disease treatment in hard clams. *J. World Mar. Soc.* 15:310–317.
- Kraeuter, J. N. & M. Castagna. 1989. Factors affecting the growth and survival of clam seed planted in the natural environment. In: J. J. Manzi & M. Castagna, editors. *Clam mariculture in North America*. Developments in aquaculture and fisheries science 19. Amsterdam: Elsevier. pp. 145–165.
- Kraeuter, J. N. & S. Ford. 1997. Clam aquaculture: improving the over winter survival of hard clams. <http://www.hsrl.rutgers.edu/clam.html>.
- Landry, T. & T. W. Sephton. 1996. Southern Gulf northern quahaug. Fisheries and Oceans Canada Atlantic fisheries stock status report, 96/102E. Maritimes Regional Advisory Process, Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada. 3 pp.
- Landry, T., T. W. Sephton & D. A. Jones. 1993. Growth and mortality of northern quahog, *Mercenaria mercenaria* (Linnaeus, 1758), in Prince Edward Island. *J. Shellfish Res.* 12:321–327.

- LeBlanc, K., M. Ouellette, G. A. Chouinard & T. Landry. 2005. Commercial harvest and population structure of a northern quahog (*Mercenaria mercenaria* Linnaeus 1758) population in St. Mary's Bay, Nova Scotia, Canada. *J. Shellfish Res.* 24:47–54.
- Loosanoff, V. L. & H. C. Davis. 1950. Conditioning *V. mercenaria* for spawning in winter and breeding its larvae in the laboratory. *Biol. Bull.* 98:60–65.
- Loosanoff, V. L. & H. C. Davis. 1963. Rearing of bivalve larvae. *Adv. Mar. Biol.* 1:1–136.
- MacKenzie, C. L., Jr., A. Morrison, D. L. Taylor, V. G. Burrell, Jr., W. S. Arnold & A. T. Wakida-Kusunoki. 2002. Quahogs in eastern North America: Part I. Biology, ecology, and historical uses. *Mar. Fish. Rev.* 64:1–55.
- MacNair, N. 2003. Overwintering trials of the notata quahaug in PEI. Aqua Info. Aqua. Notes. Prince Edward Island Dept. Fish. Aqua. Environ. AIN 13. [http://www.gov.pe.ca/photos/original/fae\\_ain13\\_2004.pdf](http://www.gov.pe.ca/photos/original/fae_ain13_2004.pdf).
- Maine Department of Marine Resources. 2007. <http://www.maine.gov/dmr/>.
- Malinowski, S. 1986. Small-scale farming of the hard clam on Long Island, New York. New York: New York State Urban Development Corporation. 60 pp.
- Murray, T. J. & J. E. Kirkley. 2005. Economic activity associated with clam aquaculture in Virginia—2004. Virginia Sea Grant (VSG-05-04). Virginia Institute of Marine Science, Gloucester Point, VA. Mar. Res. Rep. No. 2005-5 21 pp.
- Ólafsson, E. B. 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *J. Anim. Ecol.* 55:517–526.
- Pernet, F., R. Tremblay, C. Gionet & T. Landry. 2006. Lipid remodeling in wild and selectively bred hard clams at low temperatures in relation to genetic and physiological parameters. *J. Exp. Biol.* 209:4663–4675.
- Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monogr.* 52:437–475.
- Peterson, C. H., P. B. Duncan, H. C. Summerson & G. W. Safrit, Jr. 1983. A mark–recapture test of annual periodicity of internal growth band deposition in shells of hard clams, *Mercenaria mercenaria*, from a population along the southeastern United States. *Fish. Bull. (Wash. D. C.)* 81:765–779.
- Peterson, C. H., H. C. Summerson & J. Huber. 1995. Replenishment of hard clam stocks using hatchery seed: combined importance of bottom type, seed size, planting season and density. *J. Shellfish Res.* 14:293–300.
- Pettigrew, N. R., J. H. Churchill, C. D. Janzen, L. J. Mangum, R. P. Signell, A. C. Thomas, D. W. Townsend, J. P. Wallinga & H. Xue. 2005. The kinematic and hydrographic structure of the Gulf of Maine Coastal Current. *Deep-Sea Res.* 52:2369–2391.
- Pfeiffer, T. J. & K. A. Rusch. 2007. Comparison of three culture methods for the intensive culture of northern quahog seed, *Mercenaria mercenaria*. *J. World Aquacult. Soc.* 32:11–20.
- Philippakos, E., C. Adams, A. Hodges, D. Mulkey, D. Comer & L. Sturmer. 2001. Economic impact of Florida cultured hard clam industry. Florida Sea Grant publ. SGR-123, Proj. No. SGEP-12. University of Florida, Gainesville. 32 pp.
- Proctor, W. 1929. *Venus mercenaria* at Mt. Desert, Maine. *Nautilus* 42:102–103.
- Rivera, G. 2007. Culturing hard clams with greater success: a cooperative approach. New York Sea Grant. R/ATD-10: Analysis of field plantings of young cultured hard clams, *Mercenaria mercenaria* (Linne), in Long Island. Cornell Cooperative Extension, Suffolk County, Southold, NY. May 2007. 3 pp.
- Robinson, S. M. C. & T. W. Rowell. 1990. A re-examination of the incidental fishing mortality of the traditional clam hack on the soft-shell clam, *Mya arenaria* Linnaeus, 1758. *J. Shellfish Res.* 9:283–289.
- Sokal, R. R. & F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3<sup>rd</sup> edition. New York: W.H. Freeman. 887 pp.
- Townsend, D. W., N. R. Pettigrew & A. C. Thomas. 2005. On the nature of *Alexandrium fundyense* blooms in the Gulf of Maine. *Deep-Sea Res.* 52:2603–2630.
- Urban, M. C. 2007. The growth–predation risk trade-off under a growing gape-limited predation threat. *Ecology* 88:2587–2597.
- Vadas, R. L., Sr., B. D. Smith, B. Beal & T. Dowling. 2002. Sympatric growth morphs and size bimodality in the green urchin (*Strongylocentrotus droebachiensis*). *Ecol. Monogr.* 72:113–132.
- Winer, B. J., D. R. Brown & K. M. Michels. 1991. Statistical principles in experimental design. 3rd edition. New York: McGraw-Hill. 1057 pp.
- Witherspoon, N. 1984. An investigation of the aquaculture potential of the bay quahaug, *Mercenaria mercenaria*, the American oyster, *Crassostrea virginica*, and the blue mussel, *Mytilus edulis*, in three estuaries along the Northumberland Strait coast of Nova Scotia. Nova Scotia Dept. Fisheries, Halifax, NS. Manuscript and Technical Report Series, Project Report No. 84-01.79. 83 pp.
- Zar, J. H. 1999. Biostatistical analysis. 4th edition. Upper Saddle River, NJ: Prentice Hall. 663 pp.
- Zarnoch, C. B. & M. P. Schreiber. 2008. Influence of temperature and food availability on the biochemical composition and mortality of juvenile *Mercenaria mercenaria* (L.) during the over-winter period. *Aquaculture* 274:281–291.