

**Ocean-Based Nurseries for Cultured Lobster (*Homarus americanus* Milne Edwards) Postlarvae: Initial Field Experiments off the Coast of Eastern Maine to Examine Effects of Habitat and Container Type on Growth and Survival**

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Source: Journal of Shellfish Research, 31(1):167-176. 2012.

Published By: National Shellfisheries Association

DOI: <http://dx.doi.org/10.2983/035.031.0120>

URL: <http://www.bioone.org/doi/full/10.2983/035.031.0120>

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## OCEAN-BASED NURSERIES FOR CULTURED LOBSTER (*HOMARUS AMERICANUS* MILNE EDWARDS) POSTLARVAE: INITIAL FIELD EXPERIMENTS OFF THE COAST OF EASTERN MAINE TO EXAMINE EFFECTS OF HABITAT AND CONTAINER TYPE ON GROWTH AND SURVIVAL

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**ABSTRACT** The commercial fishery for American lobster *Homarus americanus* Milne Edwards in Maine has experienced the highest landings during the past 2 decades than at any time since the 1950s. However, there is no scientific consensus on why landings have increased nearly 250% from 1990 to 2010, and no one can predict how long landings can be expected to remain at current levels. This uncertainty has sparked a renewed interest in lobster stock enhancement using cultured individuals. Historically, lobster stock enhancement in North America has focused primarily on releasing early benthic phase (stage IV) animals. It is not cost-effective to feed and maintain animals in the laboratory or hatchery until they are larger (ca. stage X–XI), as is typical of enhancement efforts with cultured individuals of *Homarus gammarus* (L.) in Europe, even though survival to commercial size presumably would be greater. One difficulty with releasing early benthic phase animals is that they have the capacity to swim away from the release site, making tests to determine the efficacy of such programs logistically difficult and expensive. A low-cost, low-maintenance, ocean-based nursery grow-out system for stage IV *H. americanus* was tested in waters off eastern Maine using technology first developed and implemented successfully for cultured individuals of *H. gammarus* in Ireland. A single individual was added to a plastic soda bottle (ca. 350 mL) or Petri dish (440 mL) containing a series of small holes to allow continuous flow of seawater into and out of the units. Bottles ( $n = 630$ ) and dishes ( $n = 420$ ) were added to rigid nursery cages constructed of traditional vinyl-coated lobster trap wire and deployed in July 2002 ca. 2 m off the bottom in depths of 10 m, 15 m, and 25 m in and around Chandler Bay near Jonesport. After nearly 70 days, survival in the bottles varied from 20% at the deep-water site to 90% at the shallow-water site; however, after an additional 244–288 days, most bottles had filled with muddy sediments, and mortality rate was nearly 100%. Conversely, survival rates after 448 days in the dishes varied, on average, from 21.5–47.2% per cage originally deployed at the deepest and shallowest site, respectively. Growth rates in the dishes generally doubled during the 14-mo field trial from a carapace length of 4.2 mm to that of 8.9 mm. Results suggest that ocean nurseries can be used to rear cultured lobsters to larger sizes prior to release for stock enhancement purposes; however, these animals are too small to apply visible tags (i.e., streamer or T-bar tags) that fishers could discern easily.

**KEY WORDS:** lobster, *Homarus americanus*, culture, postlarvae, nursery, Maine, field experiment

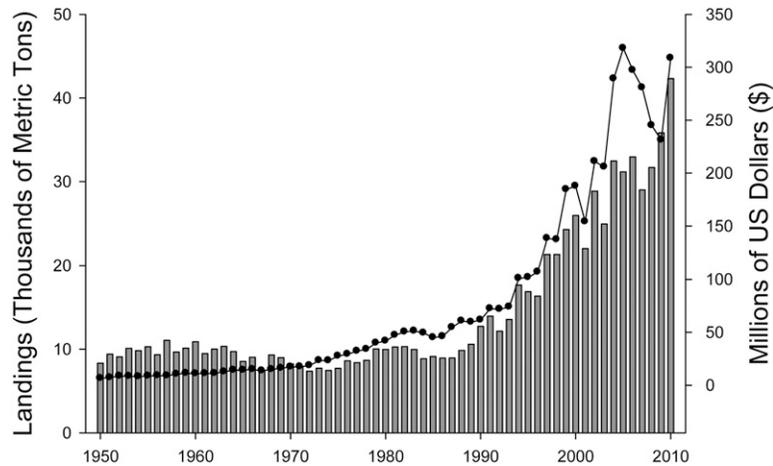
### INTRODUCTION

The American lobster, *Homarus americanus* Milne Edwards, 1837, supports one of the most lucrative commercial marine fisheries along the northeastern coast of the United States as well as the Canadian Maritimes. For example, in 2009, lobster landings accounted for 38% (US\$298.3 million) and 36% (CAN\$495.3 million) of all commercial fish species landed in New England and Atlantic Canada, respectively (Department of Fisheries and Oceans Canada 2011, National Marine Fisheries Service 2011). In Maine, the state with the highest reported landings of lobsters in the northeast United States, the value of lobster landings in 2010 was \$308.7 million, and accounted for 69% of all commercial marine species landed in that state (Maine Department of Marine Resources 2011). During the past 2 decades, the Maine lobster fishery has experienced an unprecedented surge in landings. For example, during the 40 y from 1950 to 1990, annual landings averaged 9173 mt (minimum, 8,243 mt in 1970; maximum, 11,069 mt in 1957). Since 1991, annual landings have averaged 24,740 mt (minimum, 12,170 mt in 1992; maximum, 42,311 mt in 2010), an increase of nearly 170% (Fig. 1).

The mechanism for this apparent population explosion is a matter of debate within the scientific community, especially

because the increase in landings has not occurred as a result of new management programs, rule making, or significant increases in fishing effort (Acheson & Gardner 2005). Several hypotheses have been proposed to account for the record upsurge in lobster landings in Maine. Some argue that the collapse of groundfish fisheries along the Maine coast and Gulf of Maine around the time lobster landings began their historic increase has removed several large lobster predators (cod, *Gadus morhua* L., 1758; white hake, *Urophycis tenuis* (Mitchill, 1814); and so on) from the ecosystem (Steneck & Carlton 2001, Worm & Myers 2003, Steneck et al. 2004, Wilson et al. 2007), but direct observations of gut contents from these predators argue against this hypothesis (Hanson & Lanteigne 2000, Watts & MacPherson 2002). Increasing seawater temperature has been correlated positively with lobster catch in a number of studies (Dow 1978, Koeller 1998) as well as settlement (Boudreau et al. 1992), individual growth rate (Hughes & Matthiessen 1962), and time to reach sexual maturity (Comeau & Savoie 2002, Little & Watson 2005); however, sea-surface temperature changes were not correlated with increases in lobster abundance throughout the Gulf of Maine during the period of the most rapid increase in landings (the 1980s through the mid 1990s (Acheson & Steneck 1997, Steneck & Wilson 2001)). A boom-and-bust fishery for green sea urchins (*Strongylocentrotus droebachiensis* (O. F. Müller, 1776)) occurred in Maine during the 1990s (Berkes et al. 2006). Urchins modify bottom habitats by feeding on kelp and other benthic macrophytes (Vadas et al. 1986) that lobsters may use as a spatial

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DOI: 10.2983/035.031.0120



**Figure 1.** American lobster landings (metric tons: bars) and dockside value (U.S. dollars: circles) from the Maine fishery (1950 to 2010). Landings data from the Maine Department of Marine Resources (2011).

refuge from predators, especially during molting (Johns & Mann 1987, Bologna & Steneck 1993). When fishing pressure reduced urchin densities below a critical threshold, the echinoderms could no longer control macroalgal recruitment (McNaught 1999, Steneck et al. 2004), and vast areas of Maine's nearshore marine environment shifted from herbivore-dominated barrens to lush macroalgal beds. Although this phase shift increased lobster habitat, it also created new space for small apex fish and crustacean predators that are known consumers of juvenile lobsters (Steneck et al. 2002). Another hypothesis for the dramatic upswing in lobster landings is that lobster bait (Atlantic herring, *Clupea harengus* Linnaeus, 1758) has become a significant food subsidy for juvenile lobsters, and that a positive feedback exists between fishing effort and landings (Saila et al. 2002, Grabowski et al. 2010).

It is likely that none of these hypotheses alone or others (e.g., differential settlement and recruitment of postlarvae, sensu Incze et al. (2006, 2010)) can explain fully the extraordinary increases in commercial lobster catches in northern New England and Atlantic Canada during the past 2 decades. Currently, the lobster fishery in Maine is akin to a monoculture (Wilson et al. 2007, Folke 2010) that is potentially susceptible to numerous large-scale threats that similar fisheries in southern New England and the southern Gulf of St. Lawrence have experienced associated with disease (Glenn & Pugh 2005, Pearce & Balcom 2005), introduction of nonindigenous species (Rosson et al. 2006), and continued ocean warming (Dove et al. 2005, Qadri et al. 2007).

Because it is difficult to predict whether the observed upsurge in commercial lobster landings in the northwestern Atlantic during the past 2 decades will continue, and if so for how long, there is perhaps no better time to reexamine the role of aquaculture as a fisheries management tool to enhance *H. americanus* stocks (Castro et al. 2001). Stock enhancement efforts of American lobsters began during the 1870s in Maine and Massachusetts when gravid females were placed into tidal impoundments (culturing stations) where their eggs hatched, followed by the release of stage I–IV individuals over a 3 to 4-wk period (Nicosia & Lavalli 1999). Taylor and Dow (1958) described a state-operated lobster hatchery in West Boothbay Harbor, ME, that produced and released more than 2 million stage IV juveniles

over a decade beginning in 1935. However, lacking evidence that lobster landings had improved as a result of releasing cultured juveniles, the stock enhancement program was discontinued. A similar scenario occurred in Massachusetts, where cultured stage IV lobsters produced at a state-sponsored hatchery on Martha's Vineyard were released to the wild beginning in 1949. Efforts there ceased in 1997 because, once again, there was no evidence that stock enhancement efforts had resulted in increased landings.

In Maine, interest in lobster stock enhancement grew again during the mid 1980s when a fishermen-supported hatchery in eastern Maine was created in the town of Cutler (Beal et al. 1998). That program, which released more than 100,000 stage IV animals annually and led to a modification in hatchery production technology resulting in 50–60% survival of stage I–IV lobster larvae in mass culture tanks (Beal & Chapman 2001), ceased after 8 y because of the lack of funding and data demonstrating that enhancement was effective. A more recent effort in Stonington, ME, to enhance lobster stocks with cultured stage IV animals lasted 5 y (2005 to 2009; T. Ames, Stonington, ME, pers. comm.).

To date, all stock enhancement efforts for American lobsters in the northeast United States have had one commonality—repeated releases in coastal waters of hundreds to thousands of stage IV animals at once, generally during summer months, over cobble and other heterogeneous bottoms. Because cannibalism in mass culture within the hatchery increases dramatically after stage IV (pers. obs.), and because it is costly to confine and feed small lobsters individually for even short periods of time, logistics and expenses per animal dictated the release of stage IV animals. To assess the efficacy of these enhancement programs, it is possible to use coded microwire tags (Krouse & Nutting 1990), genetic fingerprinting, and/or BACI sampling designs (Underwood 1992) to estimate density of cultured animals at some time after release. However, each method is relatively expensive, logistically complicated, and requires scientists to interpret and present data in some form to fishers. Adding to the complexity associated with evaluating hatch-and-release programs using stage IV or stage V animals is that animals at these sizes (as well as stages VI and VII) have been observed to swim (Herrick 1909, Beal pers. obs.). A method to assess the efficacy of lobster stock enhancement that would give fishers instant

information from their daily catch without the need for scientific interpretation is to release juvenile color morphs (Addison & Bannister 1994, Beal et al. 1998). However, no large-scale attempt has occurred to investigate the effectiveness of enhancing stocks of American lobster using color morphs.

It is possible to maintain juvenile lobsters in the laboratory for 3 mo or longer by confining them individually and supplying food (artificial or natural diets) regularly, as in the many enhancement efforts in Europe using cultured *Homarus gammarus* (Linnaeus, 1758) (Bannister & Addison 1998, Burton 2003). This strategy increases the cost per lobster and is not a cost-effective alternative for stock enhancement of *H. americanus* because of the relative low price per kilogram of commercial-size individuals (\$7.30/kg in Maine on average in 2010 compared with \$15.30/kg for *H. gammarus* in the United Kingdom in 2009 (Marine Management Organisation 2009)). The advantage, however, of releasing larger lobsters (stage XII and larger) to the wild is that they have a greater probability of surviving to enter the commercial fishery (Wahle 1992, Benevente et al. 2010).

Here, I present a novel method to rear postlarval American lobsters individually up to 14 mo in ocean-based nurseries without having to maintain the grow-out system or feed the lobsters, as an alternative to releasing stages IV and V animals directly to the bottom. The work focused on 2 objectives: (1) to determine whether ocean-based nursery technology used to rear cultured, postlarval *H. gammarus* successfully for nearly a year off the west coast of Ireland (Beal et al. 2002) could be replicated with cultured postlarvae of *H. americanus* in Maine; and (2) to determine whether nursery grow-out methodologies would produce animals large enough to receive and retain a visible marker, such as visual implant elastomer tag (sensu Uglem et al. 1996) or streamer tag (sensu Linnane & Mercer 1998).

## METHODS

### Study Sites

#### Intertidal Site

Because of the extensive soft-bottom intertidal habitat that exists in eastern Maine, and juvenile lobsters that have been found ubiquitously over diverse bottom types in the lower intertidal and subtidal throughout their range (Cobb 1971, Cowan 1999), 3 field experiments were conducted on an intertidal mudflat between Perio Point, Beals, ME (44°31.31' N, 66°36.52' W) and French House Island (44°31.31' N, 66°36.52' W; Fig. 2). The first (July 17–18 to August 9, 2002) occurred near the mid intertidal (0.0 m). The second (August 10 to November 7, 2002) occurred near the upper (+1 m) and lower intertidal (−0.3 m). The third (August 22 to December 12, 2002) occurred near the low intertidal. Sediments generally were poorly sorted (sensu Folk 1974), and median grain size varied inversely with tidal height (0.5φ = upper, 2.8φ = mid, 3.5φ = lower).

#### Subtidal Sites

Three field experiments were conducted subtidally within a 15-km area between Jonesport, Great Wass Island, and Roque Island in eastern Maine (Fig. 2). The first was initiated on July 31, 2002, at 3 hard-bottom sites in Chandler Bay near Ballast Island (depth, 15 m; 44°34.54' N, 67°33.08' W); Bonney

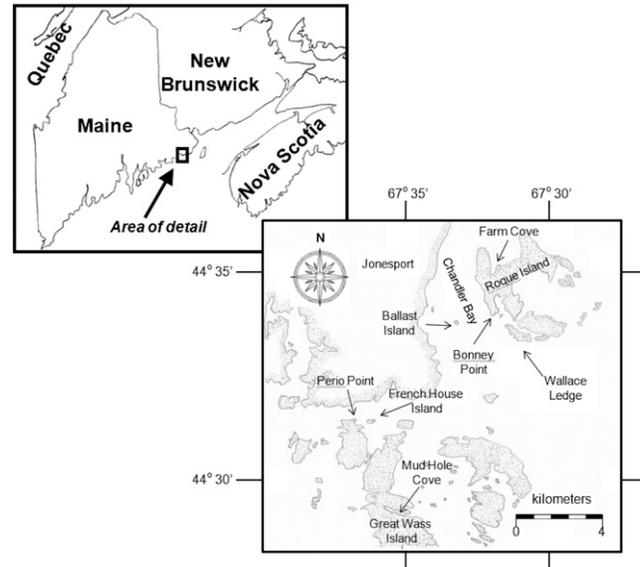


Figure 2. Subtidal and intertidal study sites in eastern Maine.

Point, near the southwestern corner of Roque Island (depth, 20 m; 44°34.64' N, 67°32.37' W), and Wallace Ledge (depth, 25 m; 44°33.24' N, 67°31.37' W). The second was initiated on hard bottom on August 2 and 20, 2002, at the mouth of Mud Hole Cove (MHC; depth, 7 m; 44°29.10' N, 67°34.54' W), on the eastern side of Great Wass Island (see Beal et al. (1995) for a description of this site; Fig. 2). The third experiment was conducted at the surface in MHC (44°29.13' N, 67°35.20' W) beginning August 6, 2002.

### Experimental Animals

All postlarval lobsters (stage IV) used in the field experiments were produced at the Beals Island Regional Shellfish Hatchery (BIRSH) located on Perio Point (Fig. 2), Beals, ME. Oviparous broodstock lobsters were collected from local fishermen in late June 2002. Releases of stage I larvae began on July 1, and larvae were reared to stage IV (early benthic phase), according to Beal and Chapman (2001), over a 16 to 18-day period. Stage IV animals not used immediately in experiments were held individually in PVC tubes (38 mm in diameter × 76 mm tall, with fiberglass window screening (aperture, 1.8 mm) glued to the bottom of each) that were placed ca. 5 mm off the bottom in shallow (50-mm) tanks with ambient, flowing seawater. Animals were fed once daily with cultured brine shrimp, *Artemia salina* (Linnaeus, 1758), that were enriched with cultured microalgae. Four separate batches of lobster larvae were reared between July 1 and August 15, 2002.

#### Intertidal Experiments (Perio Point, Beals Island)

On July 17–18, 2002, 1 stage IV lobster (mean carapace length (CL) ± 95% confidence interval, 3.96 ± 0.079 mm; mean total mass (TM) ± 95% confidence interval, 0.048 ± 0.002 g;  $n = 15$ ) was added to a 10-cm-diameter × 10-cm-deep horticultural plastic plant pot after filling either with ambient mud ( $n = 10$ ) or sand/gravel from the upper intertidal ( $n = 10$ ). Each pot was covered with a piece of fiberglass window screening that was

secured to the rim with a rubber band, and then each was pushed into the mud ( $2 \times 10$  matrix, 1-m spacing between rows and columns) near the mid intertidal so that the rim was even with the adjacent sediments. Only animals with 2 claws were used. The experiment concluded 23 days later on August 9, when pots were recovered and their contents washed through a 1-mm sieve.

On August 10, a second experiment was initiated at 2 tidal levels (upper and lower). At each tidal height, 30 10-cm-diameter pots were filled with sand/gravel from the upper intertidal (as described earlier) and arrayed in a  $6 \times 5$  matrix with 1-m spacing between rows and columns. A single stage IV lobster (2 claws) was added to the surface sediments of each pot (initial mean CL,  $4.69 \pm 0.27$  mm; initial mean TM,  $0.072 \pm 0.011$  g;  $n = 4$ ). A piece of fiberglass window screening was affixed to each pot as described earlier. Experimental units were recovered after 89 days on November 7 and processed as described earlier.

On August 22, a third experiment was initiated near the low tide level. Five blocks, each containing a  $3 \times 3$  matrix of pots (as described earlier) were deployed. Pots were filled with sand/gravel from the upper intertidal, and a single stage IV lobster (2 claws) was placed in each as described earlier (initial mean CL,  $4.68 \pm 0.28$  mm; initial mean TM,  $0.077 \pm 0.014$  g;  $n = 11$ ). Experimental units were covered with a piece of fiberglass window screening (as described earlier), recovered 112 days later on December 12, and processed as described earlier.

#### Containers for Subtidal Field Trials

Two types of containers were used in the subtidal field trials: Petri dishes (150 mm diameter  $\times$  25 mm deep; 440 mL) and recycled, plastic soda bottles (350 mL). Ten to 15 holes (diameter, 2.2 mm) were drilled in the top and bottom of each dish, and the same number of holes of approximately similar size were punched in each bottle using a hand-held awl. Prior to the addition of cultured lobsters, bottles and dishes were added to an outdoor tank receiving ambient, flowing seawater at BIRSH between June 18 to June 27 to initiate fouling in the containers, and they remained in the tank until they were used in field experiments (described later).

#### Nursery Cages for Subtidal Field Trials

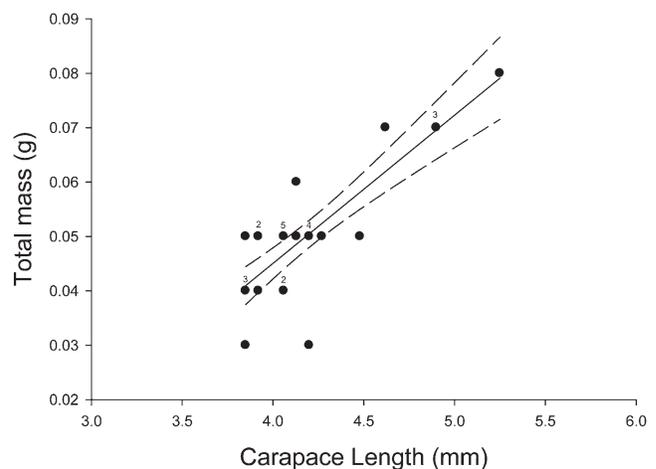
Containers with a single lobster each were added to modified, commercial-size lobster traps ( $91 \times 50 \times 45$  cm, with 2.5-cm apertures) constructed of vinyl-coated wire (12.5 gauge), hereafter called nursery cages, that were similar to those described in Beal et al. (2002). Units stood upright and were fitted with a series of 9 equidistant, horizontal shelves made from the same coated wire. A hinged door allowed access to each shelf. The door was held shut with a rubberized cord attached to a wire hook that could be pulled across the door and attached to an aperture on an adjacent side. The topmost shelf was used for buoyancy (filled with one or more pieces of Styrofoam for flotation) and the bottommost shelf was not used. Ten containers of a single type (i.e., bottles or Petri dishes) were added to each of 7 shelves per nursery cage ( $n = 70$ ). Bottles were sandwiched between 2 pieces of vinyl-coated wire mesh ( $42 \times 38$  cm) held together with nylon cable ties. Petri dishes were arrayed as 2 stacks of 5 dishes each per shelf (upper and lower stack). That is, 5 dishes were arrayed in a quincunx pattern on

a piece of wire mesh ( $42 \times 38$  cm). Another piece of wire mesh was placed over those dishes and then a second array of 5 dishes was added. A third piece of wire mesh was placed over the upper dishes. The bottommost wire mesh and the topmost wire mesh were held together tightly using several nylon cable ties.

Cages were anchored to the bottom by tying each to a plastic bucket (18.9 L) filled with cement. A 2-m piece of rope connected the bottom of each cage to an eye bolt protruding through the cement within the plastic bucket. Another piece of rope was attached to the same bolt that led to a surface float. When a cage was deployed, it sank quickly to the bottom, and then rose ca. 2 m off the bottom because of the Styrofoam pieces in the topmost shelf; therefore, cages were designed to float in the water column 2 m off the bottom (sensu Beal et al. 2002) to avoid potential contact with any sediment on the bottom. This arrangement is similar to that used by Beal et al. (1995) to overwinter juveniles of the soft-shell clam *Mya arenaria* Linnaeus, 1758.

#### Subtidal Experiments (Chandler Bay, Jonesport)

To determine whether cultured juveniles of *H. americanus* would survive and grow in field-based nursery cages, on July 31, 2002, 5 nursery cages (3 containing 70 bottles, 2 containing 70 dishes) with 1 lobster each (initial mean CL,  $4.21 \pm 0.14$  mm; initial mean TM,  $0.051 \pm 0.005$  g;  $n = 29$ ; Fig. 3) were each deployed at 3 hard-bottom, subtidal locations in Chandler Bay (Ballast Island, Bonney Point, and Wallace Ledge). Cages remained at each location until October 12, 2002, when all were sampled visually to determine percent survival, and then each was moved to shallow water (depth, 4–6 m) to avoid being moved or destroyed by seasonal (winter) sea scallop (*Placopecten magellanicus* (Gmelin, 1791)) dragging gear. Cages from Bonney Point and Wallace Ledge were moved near Farm Cove on the northeastern side of Roque Island (Fig. 2). Cages from Ballast Island were moved to water of similar depth located



**Figure 3.** Relationship between carapace length and mass of juvenile stage IV lobsters reared at the Beals Island Regional Shellfish Hatchery and used in the subtidal field trials (July 31, 2002).  $Y = -0.639 + 0.272X$  ( $r^2 = 0.711$ ,  $n = 29$ ). Dashed lines represent 95% CIs. Mean carapace length,  $4.2 \pm 0.14$  mm; mean mass,  $0.05 \pm 0.004$  g. All lobsters had both dactyls. The number above point represents the number of similar observations. Carapace length was measured using a stereomicroscope at  $1.5\times$  magnification with an ocular micrometer.

approximately 2.5 km north of Bonney Point along the Roque Island shore (Parker Head: 44°34.82' N, 67°32.54' W).

On June 13, 2003, after 317 days, all 6 cages with bottles from Farm Cove and 1 of the 3 cages with bottles from Parker Head were removed permanently from the water, and their contents were assessed for live lobsters. Forty days later, on July 23, 2003, the remaining cages containing bottles from Parker Head were removed from the water, and lobster survival was measured. On that same day, the 4 cages with Petri dishes from Farm Cove were moved to Parker Head, where they joined the 2 remaining cages with Petri dishes that had been moved from Ballast Island the previous fall. These 6 cages with Petri dishes remained at Parker Head until October 22, 2003. On that date, the total length (TL), CL, and TM of each live lobster was recorded at the Downeast Institute for Applied Marine Research and Education (DEI) near Black Duck Cove, Great Wass Island, Beals, ME (44°28.84' N, 67°35.89' W). TL was measured to the nearest 0.1 mm using Vernier calipers, whereas CL was measured to the nearest 0.01 mm using a stereomicroscope at 1.5× magnification with an ocular scale in 1 eyepiece. TM was measured to the nearest 0.01 g using a Sartorius (Acculab VIC-612, Acculab, Edgewood, NJ) digital balance.

#### *Subtidal Experiments (MHC, Great Wass Island)*

Two nursery cages were deployed near the entrance to MHC on August 2, 2002. Each cage contained 90 small, unfouled Petri dishes (100 mm diameter × 15 mm deep (ca. 120 mL), with 35 2.2-mm holes drilled in each) arrayed within wire sandwiches (as described earlier) and placed on 6 shelves per cage (15 dishes per wire sandwich). A single lobster (mean CL, 4.69 ± 0.18 mm,  $n = 21$ ; mean TM, 0.071 ± 0.064 g,  $n = 9$ ) was added to each dish. Two additional nursery cages were deployed at the same location on August 20, 2002. One cage was stocked with 210 prefouled bottles containing 1 lobster each (similar in size and mass to that described earlier) with 30 bottles on each of 7 shelves. Bottles were not sandwiched between pieces of vinyl-coated wire, but instead were forced into each shelf so that when the door was closed, bottles were held firmly in place. The other cage held 120 bottles on 4 shelves plus an additional 11 bottles on a sixth shelf.

Each of the 4 nursery cages was returned to BIRSH on October 27, 2002, and placed in an indoor flow-through holding tank (9 m long × 7.5 m wide × 1.2 m deep; 81,000 L) receiving continuous flowing, ambient seawater, where they remained over the winter. The cage with 131 bottles was sampled on November 7, 2002.

#### *Laboratory Controls*

Beginning August 27, 2002, survival of hatchery-reared, early benthic phase lobsters was determined over 36 wk under laboratory conditions at the Aquaculture Research Facility at the University of Maine at Machias. A single lobster (mean CL, 4.59 ± 0.18 mm;  $n = 20$ ) was added to a plastic cup (350 mL) with 35 holes (2.2 mm). Nine cups were positioned into holes (diameter, 10 cm) cut out of a circular piece of household Styrofoam. The arrangement of cups and Styrofoam were added to each of 11 40-L, round-bottom kreisels filled with 35 L seawater (5-µm filtered stock from BIRSH). A relatively constant temperature of 16 ± 1°C was maintained during the experimental period. Each kreisel was aerated gently from the bottom, and seawater in each was changed every 4 wk. During

seawater changes, kreisels were cleaned with a mild soap and warm freshwater. Animals were removed from cups for less than a minute, and cups cleaned with warm freshwater on the dates when kreisels were cleaned. Animals were fed *ad libitum* an Orion fish feed dry pellet (3.5 mm; Skretting Canada) developed for Atlantic salmon juveniles (see Sutherland et al. (2006) for analysis of pellets for inorganic content, total carbon, total nitrogen, and zinc contents as well as stable carbon and nitrogen isotopes).

#### *Floating Tray Experiment (Mud Hole Cove, Great Wass Island)*

On August 6, 2002, 108 prefouled bottles containing a single juvenile lobster each with the same mean CL and TM as described in the previous section were added to each of 3 wooden trays (1.22 m × 0.91 m × 6.25 cm deep) lined completely with fiberglass window screening. A sheet of black plastic (1.2 mm thick) was placed over the top of each tray to deter herring and great black-backed gulls (*Larus argentatus* Pontoppidan, 1763, and *Larus marinus* Linnaeus, 1758, respectively) from poking their beaks through the window screening (Beal, pers. obs.), and each was deployed at the surface of MHC. Trays were returned to BIRSH on October 27, 2002, and placed in a flow-through holding tank (described earlier). The contents of each were inspected approximately 1 y later, on October 1, 2003 (421 days).

#### *Statistical Analyses*

For the 3 intertidal experiments and Chandler Bay subtidal experiment involving cages with plastic bottles, no statistical analyses were warranted (see Results). A 3-way factorial analysis of variance (ANOVA) was performed on the square root-transformed number of lobster juveniles surviving in a sandwich of nursery cages stocked with Petri dishes. Each factor was fixed, and included site of original deployment (Ballast Island, Bonney Point, Wallace Ledge), shelf level (7 per cage), and level in the wire sandwich where dishes were located (i.e., top stack vs. bottom stack). Analysis of covariance (ANCOVA) was performed on the ln-transformed mass-length data for all surviving lobsters with 2 claws to determine potential differences in morphology between sites of original deployment.

## RESULTS

#### *Intertidal Experiments*

A total of 8 lobsters were recovered alive from the first experiment, all from units filled with sediments from the upper intertidal (mean CL, 4.94 ± 0.183 mm; mean TM, 0.083 ± 0.011 g). Lobsters had increased approximately 25% in CL and 75% in TM during the 23-day trial, suggesting that at least 1 molt had occurred during the period. No lobsters were recovered alive from experimental units in either of the other 2 experiments.

#### *Subtidal Experiments (Chandler Bay, Jonesport)*

##### **July 31 to October 12, 2002 (73 days)**

Survival after 73 days in the nursery cages containing bottles varied between 20% and 40% at Wallace Ledge. Many bottles had begun to fill with muddy sediments, and several were found to contain lobsters in a weakened state. Many animals appeared pale in color, and were lethargic when removed from the bottles

and placed into shallow pans with clean seawater. Survival in the Petri dishes was not assessed at this site. The outside of all containers was lightly fouled, mostly with an unidentified stalked ascidian. Lobster survival at Bonney Point was approximately 50% in both types of containers, although bottles appeared to house more muddy sediments than Petri dishes. Survival varied between 70% and 90% at Ballast Island. All containers were fouled more heavily than those at Wallace Ledge or Bonney Point, with barnacles (*Semibalanus balanoides* (Linnaeus, 1767)), blue mussels (*Mytilus edulis* Linnaeus, 1758), and jingle shells (*Anomia simplex* D'Orbigny, 1842), and little evidence of mud was observed inside bottles or Petri dishes. Many of the live animals had recently molted because they were a brilliant red color compared with a darker brown coloration (indicating intermolt individuals) observed in many of the containers at Bonney Point and Wallace Ledge.

**July 31, 2002 to June 13, 2003 (317 days), and to July 23, 2003 (357 days): Bottles**

No lobsters were found alive in any of the 7 cages ( $n = 490$  bottles) on June 13, 2002. Most bottles had filled completely with muddy sediments, and there was no evidence of any lobsters (e.g., molts, missing appendages). When the 2 remaining cages ( $n = 140$  bottles) were sampled on July 23, 2003, a single lobster was found alive, and it did not appear to have increased significantly in size (CL, 4.9 mm).

**July 31, 2002 to October 22, 2003 (448 days): Petri Dishes**

Overall survival in the 6 nursery cages housing juvenile lobsters in Petri dishes varied from 21.5–47.2%; however, these rates depended on where the cage had been deployed originally ( $P = 0.0157$ ) and whether dishes were arrayed on the top or bottom stack of the wire sandwich ( $P < 0.0001$ ; Table 1). Cages deployed originally at Ballast Island had ca. 33% and 97% more lobsters than those deployed at Bonney Point and Wallace Ledge, respectively (95.7% of the variation in mean survival per cage was explained by water depth at the 3 sites;  $F = 22.06$ ,  $df = 1, 1$ ,  $P = 0.1335$ ). Mean number of lobsters ( $\pm 95\%$  CI) was ca. 130% greater in the upper ( $2.29 \pm 1.87$  individuals;  $n = 42$ ) versus lower ( $1.00 \pm 0.68$  individual;  $n = 42$ ) stack in the sandwiches. Although not quantified, lobster survival appeared directly related to the volume of mud that had filled the dishes. Those filled completely with mud (many from the lower sandwich in each stack) generally lacked a live lobster, whereas lobsters generally were alive in many of the dishes without sediment or containing a small volume of sediments.

Mean CL more than doubled during the experimental period, increasing ca. 110% ( $4.21 \pm 0.14$  mm,  $n = 29$  to  $8.87 \pm 0.14$  mm,  $n = 134$ ). Mean TM increased 9-fold ( $0.051 \pm 0.005$  g,  $n = 29$  vs.  $0.458 \pm 0.023$  g,  $n = 138$ ). Mean CL varied significantly among the 6 nursery cages ( $P < 0.0001$ ), as lobsters from the Ballast Island and Wallace Ledge cages ( $9.18 \pm 0.16$  mm,  $n = 92$ ) were ca. 12% larger than those originally deployed at Bonney Point ( $8.18 \pm 0.15$  mm,  $n = 42$ ). Mean TM varied similarly among nursery cages ( $P < 0.0001$ ), as animals from the Ballast Island and Wallace Ledge cages ( $0.500 \pm 0.027$  g,  $n = 92$ ) were approximately 37% heavier than those from Bonney Point ( $0.364 \pm 0.024$  g,  $n = 42$ ).

The relationship between mass and length for all animals with 2 claws ( $n = 134$  of 159) was curvilinear (Fig. 4). The addition of a quadratic term to a linear model explained significantly more

**TABLE 1.**  
**Number of live juvenile lobsters in Petri dishes in each of 6 nursery cages collected from Parker Head near Roque Island, Jonesport, ME, on October 22, 2003, 448 days after deployment.**

Origin*	Level	(1) Upper Stack†	(1) Lower Stack†	(2) Upper Stack†	(2) Lower Stack†
Wallace Ledge	Bottom	1	2	0	1
	6	0	1	1	0
	5	2	0	1	1
	4	4	0	2	0
	3	1	1	3	0
	2	0	1	2	2
	Top	3	0	1	1
	Total	11	5	10	5
	Percent alive	31.4%	14.3%	28.6%	14.3%
Bonney Point	Bottom	0	0	1	2
	6	1	0	2	1
	5	1	1	2	2
	4	1	0	1	1
	3	4	3	2	0
	2	3	0	4	1
	Top	3	3	4	3
	Total	13	7	16	10
	Percent alive	37.1%	20.0%	45.7%	28.6%
Ballast Island	Bottom	4	1	2	0
	6	3	1	3	1
	5	3	0	5	1
	4	3	1	4	0
	3	3	0	3	2
	2	3	1	4	2
	Top	3	3	3	3
	Total	22	7	24	9
	Percent alive	62.8%	20.0%	68.6%	25.7%

\* Site of initial deployment on July 31, 2002 (see Methods).

† (1) or (2) refers to nursery cage replicate.

Five dishes each were sandwiched in an upper and lower stack on each of 7 shelves (levels) in a nursery cage, with 1 stage IV lobster per dish. ANOVA on the square root-transformed number per stack indicated a significant effect resulting from origin ( $P = 0.0157$ ) and location (upper stack vs. lower stack) in the wire sandwich ( $P < 0.0001$ ).

variation between the 2 variables ( $P < 0.0001$ ,  $r^2 = 0.9121$ ;  $Y = 1.18 - 0.317X + 0.026X^2$ ). An analysis of regression lines on the ln-transformed mass-length data from each site demonstrated equal slopes ( $F = 1.94$ ;  $df = 2, 128$ ;  $P = 0.1475$ ), and ANCOVA showed no site effect ( $P = 0.0644$ ), suggesting that the morphology of animals was similar between sites of original deployment.

**Subtidal Experiments (Mud Hole Cove, Great Wass Island; August 2 and 20 to November 7 2002)**

The nursery cage deployed on August 20, 2002, with 131 bottles was sampled on November 7, 2002, after residing in the tank house at Perio Point in flowing, ambient seawater for 12 days. Overall survival during the 79-day period was 87.0% (114 of 131). Survival varied between 76.7% and 100%, depending on the level (i.e., shelf) on which animals were placed (topmost, 23/30 = 76.7%; second level, 25/30 = 83.3%; third level, 28/30 = 93.3%; fourth level, 27/30 = 90%; fifth level, 11/11 = 100%).

Lobsters in the remaining 3 cages were exposed to severe conditions in the tank house during February 2003. At some point

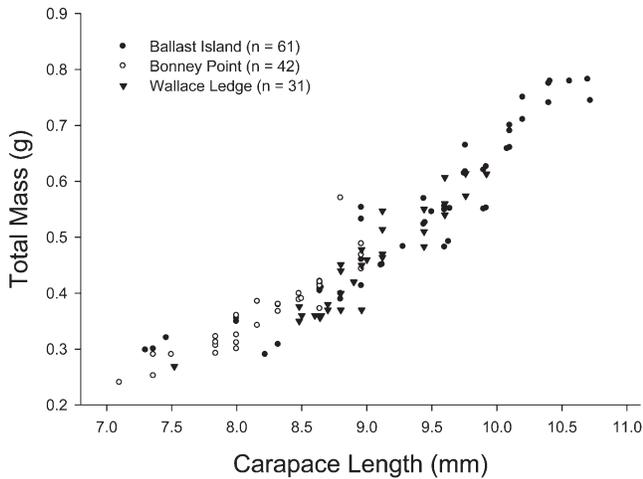


Figure 4. Relationship between carapace length and total mass for 2-clawed animals surviving in Petri dishes arrayed in 3 nursery cages. Ballast Island, Bonney Point, and Wallace Ledge represent sites where cages were deployed initially on July 31, 2002. Cages were subsequently moved to shallow-water sites on October 12, 2002, where they remained until October 22, 2003. Regression analysis on the natural log-transformed mass-length data indicated that the 3 separate lines were parallel ( $P = 0.1475$ ). Subsequent ANCOVA demonstrated no site effect ( $P = 0.0644$ ). The power exponential equation developed from the natural logarithm-transformed regression for all 134 points is as follows:  $\text{Mass} = (0.0008)(\text{CL}^{2.8619})$ ;  $r^2 = 0.901$ ,  $P < 0.0001$ .

near the middle of that month, the pump that supplied ambient seawater to the tank failed, and the seawater in the tank froze from the surface to a depth of 0.75 m. The pump was repaired, and seawater continued to flow into the tank in late February 2003. Cages were inspected in April 2003, and no live lobsters were recovered.

#### Laboratory Controls

Animals exhibited a steady mortality rate during the 36 wk from August 27, 2002 to May 5, 2003 (Fig. 5). Approximately one half of the animals had died by week 25. No lobsters remained alive after May 5, 2003. Most of the deaths appeared to be associated with molting, as animals either would begin—but not complete—ecdysis before expiring, or would die within a week or two after molting. Animals averaged  $1.58 \pm 0.20$  molts ( $n = 99$ ) before dying, with the highest frequency of 2 molts occurring in approximately 35% of the animals (Fig. 6).

#### Floating Tray Experiment (Mud Hole Cove, Great Wass Island)

Most animals in the floating trays suffered the same fate in the tank house during the winter as the lobsters in the nursery cages that had been stored at that same location. On October 24, 2003 (444 days after deployment), the 3 trays were transported from the holding tank at Perio Point to DEI. Every one of the 108 bottles in each of the 3 trays lined with fiberglass window screening was filled with mud, and no animals were found alive in any bottle. However, a single animal was found loose in the corner of each tray, which had apparently escaped from one of the bottles (some holes punched with the awl were apparently larger than 2.2 mm, enabling small lobsters to escape). Once bottles were removed from each tray, inspection of

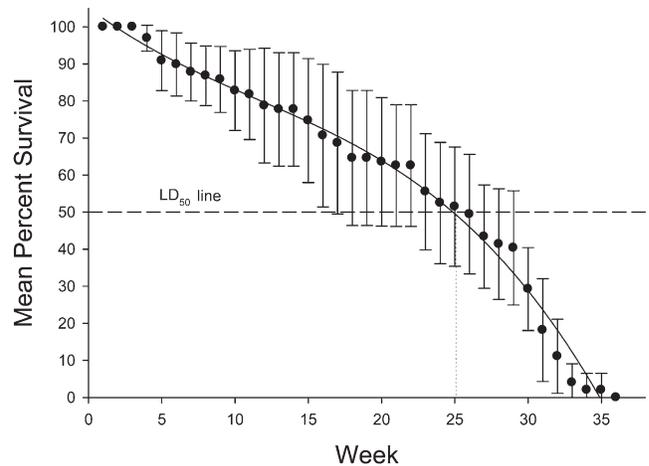


Figure 5. Mean percent survival ( $\pm 95\%$  CI) of cultured lobsters (initial mean carapace length,  $4.6 \pm 0.18$  mm;  $n = 20$ ) held in 40-L kreisels at the University of Maine at Machias (August 27, 2002 (week 1), to May 5, 2003 (week 36)). Animals were fed exclusively on salmon fish feed (3.5-mm dry pellet; Skretting Canada). Death in 50% of the animals occurred at approximately week 25 (February 12 to 18, 2003).

the remaining space revealed patches of thick mud as well as several polychaete worms (*Amphitrite cirrata* [O. F. Müller, 1771]) of variable size (i.e., adults and juveniles) and numerous juvenile blue mussels. Each of the 3 lobsters was approximately the same size, which was nearly twice as long and 10 times heavier than lobsters from Petri dishes from the subtidal experiments in Chandler Bay (CL<sub>1</sub>, 19.8 mm; TM<sub>1</sub>, 5.446 g; TL<sub>1</sub>, 78.3 mm; CL<sub>2</sub>, 18.8 mm; TM<sub>2</sub>, 4.727 g; TL<sub>2</sub>, 78.3 mm; CL<sub>3</sub>, 18.7 mm; TM<sub>3</sub>, 4.612 g; TL<sub>3</sub>, 76.1 mm; Fig. 7).

## DISCUSSION

Results demonstrated unequivocally that cultured, juvenile (stage IV) lobsters can survive for periods of up to 14 mo without intervention (feeding or other maintenance) in flow-through containers housed in ocean-based wire cages (nurseries) in eastern Maine. Survival in some Petri dishes (i.e., Ballast

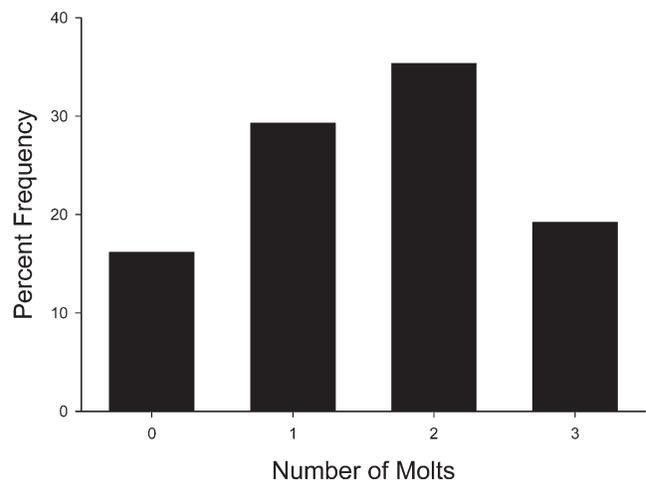


Figure 6. Frequency of molting during the laboratory experiment. Mean,  $1.58 \pm 0.20$  molts ( $n = 99$ ).



**Figure 7.** The larger juvenile lobster was 1 of 3 animals that survived in floating wooden trays lined completely with fiberglass window screening initially deployed on the surface waters of Mud Hole Cove on August 6, 2002 (carapace length (CL), 19.8 mm; total length (TL), 78.3 mm; total mass (TM), 5.446 g). It is 445 days old postdeployment. The smaller lobster in the photograph (CL, 9.8 mm; TL, 37.6 mm; TM, 0.592 g) is one of the animals that survived in a Petri dish from the Chandler Bay subtidal field experiments. It is 451 days old postdeployment. Photograph taken on October 25, 2003.

Island), especially those in the upper portion of each stack (Table 1), was similar (>55%) to that observed by Beal et al. (2002) with similar-size cultured European lobsters, *H. gammarus*, held in nursery cages for 10 mo off the west coast of Ireland.

Highest mortalities (nearly 100%) were observed in the 350-mL plastic bottles; however, initial sampling for the subtidal experiments in Chandler Bay and those from MHC suggest that survival rates greater than 70% were achieved in shallow water (Ballast Island and outer MHC) ca. 70 days after the experiments were initiated. A working hypothesis is that the mortality observed in the bottles was a result of a lack of sufficient exchange of seawater in and out of the bottles. It appears that bottles, especially, acted as sediment traps because of the insufficient number of holes, but so, too, did a large number of Petri dishes, especially those that were on the bottommost portion of the stack. Future studies should attempt to vary flow rates in and out of bottles by varying the number of holes per bottle. Although juvenile lobsters can live (burrow) in soft sediments (Botero & Atema 1982), and can apparently live for at least short durations in intertidal soft sediments (the current study), it appears that during the entire experimental period, the rate of deposition of soft sediments in nearly all the bottles was too high for small juveniles to survive for long periods either because the increased sediment load lead to a decrease in dissolved oxygen within the bottles (and they suffocated) and/or it affected negatively their food supply (and they starved).

Lobsters in the Petri dishes generally doubled in CL (from 4.2–8.9 mm) during the 14-mo field trial, although the scope for growth apparently is much greater, as evidenced by the difference in the mean size of the 3 animals that survived in the floating trays under less than optimal conditions ( $\bar{x}_{CL}$ , 19.1 mm; Fig. 7). If tagging results from juvenile *H. gammarus* (Linnane & Mercer 1998) are any indication, juvenile *H. americanus* individuals grown in the Petri dishes would be too small to accept

a streamer tag, and rate of survival for animals receiving elastomer tags may be too low to be cost effective. Although other methods are available to assess the efficacy of lobster stock enhancement using cultured individuals (microwire tagging, DNA fingerprinting, BACI sampling designs), these methods may be too cost prohibitive for large-scale, community-based enhancement programs (R. Wahle, University Maine at Orono, pers. comm.). The number of lobster fishers in Maine is several orders of magnitude greater than the number of lobster scientists. Therefore, it would seem reasonable to focus on grow-out methods that would result in animals large enough to apply streamer or other visually obvious tags so that fishers can participate directly in collecting mark–recapture results.

This study, and those conducted in Europe by Beal et al. (2002) and Benevente et al. (2010), confirmed the basic premise that it is possible to grow lobsters in some type of ocean-based nursery container without feeding and with minimal maintenance. The mechanism relating to survival and growth remains unclear, however. None of the designs used here could be used to determine whether animals survive and grow by filtering zooplankton from the water column, by feeding on recently settled macro- or meiofauna, or both. Observations suggest that lobsters fed from animals and macroalgae that fouled the inside of the Petri dishes and bottles, because fouling fauna and flora appeared to be greater in density/biomass on the outside versus the inside of the containers. In addition, lobsters apparently molted once during the first intertidal study, increasing an average 25% in CL and 75% in TM during the 23-day trial. Animals may have consumed benthic meiofauna or detritus and other particles that fell into the experimental units through the fiberglass window screening.

Although a detailed economic analysis is beyond the scope of this study, costs (\$US) of a single cage (\$90), plus the other nursery equipment (14 wire meshes per cage to hold dishes in place (\$35), 70 dishes per cage (\$2.50 per dish), rope/buoy/anchor (\$15)) was \$315. Because equipment can be reused for at least 5 y (B. Beal, pers. obs.), the yearly cost per cage is ca. \$65. Cost to produce cultured American lobsters at DEI is ca. \$0.50 per individual, or \$35 per cage. At survival rates between 40% and 60% (Table 1), the cost per lobster per year to attain CLs of nearly 9 mm would be \$3.57 to \$2.38, respectively. In 2010, Maine lobster fishers received an average price of \$3.31 for a 1-lb (0.45-kg) lobster (Maine Department of Marine Resources 2011). Therefore, for these efforts to be commercially meaningful, survival of animals produced in the ocean-based nurseries to the commercial fishery (minimum of 82.6 mm CL in Maine) would have to be nearly 100%. Future efforts should focus on maximizing growth and survival under nursery conditions, and reducing costs associated with mass culture in the hatchery.

These results have at least 2 applications. The first is for enhancement of public, commercial lobster stocks. Although production rates for the Maine fishery are at historic levels, it is unclear why landings and stock biomass are so high. Because the lobster fishery represents more than 65% of the value of all marine resources in Maine, some believe it to be a monoculture (Wilson et al. 2007). If lobster landings in Maine were to return to the 40-y average of 10,000 metric tons (1950 to 1990; Fig. 1), many fishers and other integral components of the fishery (dealers, wholesalers, shippers, as well as the bait industry) would face economic hard times. Lobster culture and nurseries may provide some insurance against a decrease in landings. Although the

lobster industry in Maine apparently is resilient to biotic and abiotic changes that affect spawning potential and catch-per-unit effort (Steneck 2006), the commercial fishery for lobster in Long Island Sound and elsewhere in southern New England has collapsed (Pearce & Balcom 2005). Lobster nurseries may be a viable approach to enhancing wild stocks in that region. The second application may be as a commercial product that could be marketed and sold either as an aquarium (pet) item or for human consumption. Lobster juveniles survive well when reared at room temperatures (ca. 20–23°C (Beal & Chapman 2001)), and the marine environment inhabited by wild *H. americanus* varies from 0–25°C (Lawton & Lavalli 1995). It is possible to rear juveniles for more than 2 y (B. Beal, pers. obs.) in tabletop aquaria (18–38 L) that are used typically to grow tropical fish. Given a relaxation of the laws in the state of Maine and elsewhere in the United States that make it illegal to possess juvenile lobsters, lobster nurseries could be used to produce a variety of different sizes of cultured *H. americanus* that could supply an already lucrative pet trade for similar-looking marine crustaceans (e.g., snapping shrimp, *Alpheus* spp.; Debelius' reef lobster, *Enoplometopus debelius* Holthius, 1983; and the blue

spiny lobster, *Panulirus versicolor* (Latreille, 1804)). Lobster growth in a nursery cage may be limited by the size of the flow-through container, as it is in static, indoor systems (Van Olst & Carlberg 1978). If it is possible to rear animals in nursery cages to a precommercial size similar to that of a commercial crawfish, *Procambarus clarkii* (Girard, 1852) (McClain & Romaine 2004), then it also may be possible to diversify the existing commercial fishery through aquaculture technology.

#### ACKNOWLEDGMENTS

This work benefitted greatly from the efforts of J. Robish and B. Gennaco, who produced the larval and juvenile lobsters at BIRSH (July to August 2002). I thank D. Proulx and K. Proulx for their help in assembling and rigging the nursery cages, and D. Proulx for helping deploy, sample, and retrieve the cages from his F/V *Starlight*. This study was funded by a grant from the Maine Technology Institute to the Downeast Institute for Applied Marine Research & Education. The University of Maine at Machias provided travel funds for the project under account 4-2-11240-480.

#### LITERATURE CITED

- Acheson, J. M. & R. J. Gardner. 2005. Spatial strategies and territoriality in the Maine lobster industry. *Ration. Soc.* 17:309–341.
- Acheson, J. M. & R. S. Steneck. 1997. Examining the bust then boom in the Maine lobster industry: the perspectives of fishermen and biologists. *North Am. J. Fish. Manage.* 17:826–847.
- Addison, J. T. & R. C. Bannister. 1994. Re-stocking and enhancement of clawed lobster stocks: a review. *Crustaceana* 67:131–155.
- Bannister, R. C. A. & J. T. Addison. 1998. Enhancing lobster stocks: a review of recent European methods, results, and future prospects. *Bull. Mar. Sci.* 62:369–387.
- Beal, B. F. & S. R. Chapman. 2001. Methods for mass rearing stages I–IV larvae of the American lobster, *Homarus americanus* H. Milne Edwards, 1837, in static systems. *J. Shellfish Res.* 20:337–346.
- Beal, B. F., S. R. Chapman, C. Irvine & R. C. Bayer. 1998. Lobster (*Homarus americanus*) culture in Maine: a community-based, fishermen-sponsored public stock enhancement program. In: L. Gendron, editor. Proceedings of a workshop on lobster stock enhancement held in the Magdalen Islands (Quebec) from October 29th to 31st 1997. Canadian Industry Report of Fisheries in Aquatic Sciences. Ottawa: Fisheries and Oceans Canada. pp. 47–54.
- 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., J. P. Mercer & A. O'Conghaile. 2002. Survival and growth of hatchery-reared individuals of the European lobster, *Homarus gammarus* (L.), in field-based nursery cages on the Irish west coast. *Aquaculture* 210:137–157.
- Benevente, G. P., I. Uglem, R. Browne & C. M. Balsa. 2010. Culture of juvenile European lobster (*Homarus gammarus* L.) in submerged cages. *Aquacult. Int.* 18:1177–1189.
- Berkes, F., T. P. Hughes, R. S. Steneck, J. A. Wilson, D. R. Bellwood, R. Crona, C. Folke, L. H. Gunderson, H. M. Leslie, J. Norberg, M. Nyström, P. Olsson, H. Österblom & M. Scheffer & B. Worm. 2006. Globalization, roving bandits, and marine resources. *Science* 311:1557–1558.
- Bologna, P. A. X. & R. S. Steneck. 1993. Kelp beds as habitat for American lobster *Homarus americanus*. *Mar. Ecol. Prog. Ser.* 100:127–134.
- Botero, L. & J. Atema. 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. *J. Crustac. Biol.* 2:59–69.
- Boudreau, B., Y. Simard & E. Bourget. 1992. Influence of a thermocline on vertical distribution and settlement of post-larvae of the American lobster *Homarus americanus* Milne Edwards. *J. Exp. Mar. Biol.* 162:35–49.
- Burton, C. A. 2003. Lobster hatcheries and stocking programmes: an introductory manual. Seafish report SR552. Edinburgh, Scotland: Sea Fish Industry Authority. 98 pp.
- Castro, K. M., S. J. Cobb, R. A. Wahle & J. Catena. 2001. Habitat addition and stock enhancement for American lobsters, *Homarus americanus*. *Mar. Freshw. Res.* 58:1253–1261.
- Cobb, J. S. 1971. The shelter related behavior of the lobster, *Homarus americanus*. *Ecology* 52:108–115.
- Comeau, M. & F. Savoie. 2002. Maturity and reproductive cycle of the female American lobster, *Homarus americanus*, in the southern Gulf of St. Lawrence, Canada. *J. Crustac. Biol.* 22:762–774.
- Cowan, D. F. 1999. Method for assessing relative abundance, size distribution, and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal zone. *J. Crustac. Biol.* 19:738–751.
- Department of Fisheries and Oceans Canada. 2011. Commercial fisheries landings, seafisheries, 2009 value of Atlantic coast commercial landings. <http://www.dfo-mpo.gc.ca/stats/commercial/land-debarq/sea-maritimes/s2009av-eng.htm>.
- Dove, A. D. M., B. Allam, J. J. Powers & M. S. Sokolowski. 2005. A prolonged thermal stress experiment on the American lobster, *Homarus americanus*. *J. Shellfish Res.* 24:761–765.
- Dow, R. L. 1978. Effects of sea-surface temperature cycles on landings of American, European and Norway lobsters. *J. Cons. Int. Explor. Mer.* 38:271–272.
- Folk, R. L. 1974. Petrology of sedimentary rocks, 2nd edition. Austin, TX: Hemphill's. 170 pp.
- Folke, C. 2010. How resilient are ecosystems to global environmental change? *Sustain. Sci.* 5:151–154.
- Glenn, R. P. & T. Pugh. 2005. Observations on the chronology and distribution of lobster shell disease in Massachusetts coastal waters. In: M. Tlusty, H. Halvorson, R. Smolowitz & U. Sharma, editors. State of

- lobster science: lobster shell disease workshop. Aquatic forum series final report 05-1. Boston, MA: New England Aquarium. pp. 141–155.
- Grabowski, J. H., E. J. Clesceri, A. J. Baukus, J. Gaudette, M. Weber & P. O. Yund. 2010. Use of herring bait to farm lobsters in the Gulf of Maine. *PLoS ONE* 5:e10188.
- Hanson, J. M. & M. Lanteigne. 2000. Evaluation of Atlantic cod predation on American lobster in the southern Gulf of St. Lawrence, with comments on other potential fish predators. *Trans. Am. Fish. Soc.* 129:13–29.
- Herrick, F. H. 1909. Natural history of the American lobster. *B. U.S. Bureau Fish.* 29:149–408.
- Hughes, J. T. & G. C. Matthiessen. 1962. Observations on the biology of the American lobster, *Homarus americanus*. *Limnol. Oceanogr.* 7: 414–421.
- Incze, L. S., R. A. Wahle, N. Wolff, C. Wilson, R. Steneck, E. Annis, P. Lawton, H. Xue & Y. Chen. 2006. Early life history and a modeling framework for lobster (*Homarus americanus*) populations in the Gulf of Maine. *J. Crustac. Biol.* 26:555–564.
- Incze, L., H. Xue, N. Wolff, D. Xu, C. Wilson, R. Steneck, R. Wahle, P. Lawton, N. Pettigrew & Y. Chen. 2010. Connectivity of lobster (*Homarus americanus*) populations in the coastal Gulf of Maine: part II. Coupled biophysical dynamics. *Fish. Oceanogr.* 19:1–20.
- Johns, P. M. & K. H. Mann. 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Biol. Ecol.* 109:275–285.
- Koeller, P. 1998. Influence of temperature and effort on lobster catches at different temporal and spatial scales and the implications for stock assessments. *Fish Bull.* 97:62–70.
- Krouse, J. S. & G. E. Nutting. 1990. Evaluation of coded microwire tags inserted in the legs of small juvenile American lobsters. *Am. Fish. Soc. Symp.* 7:304–310.
- Lawton, P. & K. Lavalli. 1995. Postlarval, juvenile, adolescent, and adult ecology. In: J. R. Factor, editor. *Biology of the lobster Homarus americanus*. San Diego, CA: Academic Press. pp. 47–88.
- Linnane, A. & J. P. Mercer. 1998. A comparison of methods for tagging juvenile lobsters (*Homarus gammarus* L.) reared for stock enhancement. *Aquaculture* 163:195–202.
- Little, S. A. & W. H. Watson, III. 2005. Differences in the size at maturity of female American lobsters, *Homarus americanus*, captured throughout the range of the offshore fishery. *J. Crustac. Biol.* 25:585–592.
- Maine Department of Marine Resources. 2011. Maine 2010 landings (live pounds) by species. <http://www.maine.gov/dmr/commercial-fishing/MaineLandingsBySpecies.pdf>.
- Marine Management Organisation. 2010. UK Sea Fisheries Statistics 2009. <http://marinemangement.org.uk/fisheries/statistics/documents/ukseafish/2009/final.pdf>.
- McClain, W. R. & R. P. Romaine. 2004. Crawfish culture: a Louisiana aquaculture success story. *World Aquacult.* 35:31–35, 60–61.
- McNaught, D. C. 1999. The indirect effects of macroalgae and micro-predation on the post-settlement success of the green sea urchin in Maine. PhD diss., University of Maine at Orono. 161 pp.
- National Marine Fisheries Service. 2011. Annual commercial landings statistics. [www.st.nmfs.noaa.gov/st1/commercial/index.html](http://www.st.nmfs.noaa.gov/st1/commercial/index.html).
- Nicosia, F. & K. Lavalli. 1999. Homarid lobster hatcheries: their history and role in research, management, and aquaculture. *Mar. Fish. Rev.* 61:1–57.
- Pearce, J. & N. Balcom. 2005. The 1999 Long Island Sound lobster mortality event: findings of the comprehensive research initiative. *J. Shellfish Res.* 24:691–697.
- Qadri, S. A., J. Camancho, H. Wang, J. R. Taylor, M. Grosell & M. K. Worden. 2007. Temperature and acid–base balance in the American lobster *Homarus americanus*. *J. Exp. Biol.* 210:1245–1254.
- Rosson, M. A., P. J. Williams, M. Comeau, S. C. Mitchell & J. Apaloo. 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). *J. Exp. Mar. Biol. Ecol.* 329:281–288.
- Saila, S. B., S. W. Nixon & C. A. Oviatt. 2002. Does lobster trap bait influence the Maine inshore trap fishery? *North Am. J. Fish. Manage.* 22:602–605.
- Steneck, R. S. 2006. Is the American lobster, *Homarus americanus*, overfished? A review of overfishing with an ecologically based perspective. *Bull. Mar. Sci.* 78:607–632.
- Steneck, R. S. & J. T. Carlton. 2001. Human alterations of marine communities: students beware! In: M. Bertness, S. Gaines & M. Hay, editors. *Marine community ecology*. Sunderland, MA: Sinauer Press. pp. 445–468.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes & M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29: 436–459.
- Steneck, R. S., J. Vavrinc & A. V. Leland. 2004. Accelerating trophic level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems (NY)* 7:323–331.
- Steneck, R. S. & C. J. Wilson. 2001. Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Mar. Freshw. Res.* 52:1303–1319.
- Sutherland, T. F., L. C. Amos, C. Ridley, I. G. Droppo & S. A. Petersen. 2006. The settling behavior and benthic transport of fish feed pellets under steady flows. *Estuaries Coasts* 29:810–819.
- Taylor, C. C. & R. L. Dow. 1958. Maine's king lobster. Augusta, ME: Maine Department of Sea Shore Fisheries. 43 pp.
- Uglen, I., H. Ness, E. Farestveit & K. E. Jorstad. 1996. Tagging of juvenile lobsters (*Homarus gammarus* (L.)) with visible implant fluorescent elastomer tags. *Aquacult. Engineer.* 15:499–501.
- Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J. Exp. Mar. Biol. Ecol.* 161:145–178.
- Vadas, R. L., R. W. Elner, P. E. Garwood & I. G. Babb. 1986. Experimental evaluation of aggregation behavior in the sea urchin *Strongylocentrotus droebachiensis*. *Mar. Biol.* 90:433–448.
- Van Olst, J. M. & J. M. Carlberg. 1978. The effects of container size and transparency on growth and survival of lobsters cultured individually. *Proc. World Maricult. Soc.* 9:469–479.
- Wahle, R. A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. *Oikos* 65:52–60.
- Watts, H. J. & H. C. MacPherson. 2002. White hake (*Urophycis tenuis*) predation on juvenile American lobster (*Homarus americanus*) in St. Georges Bay, Nova Scotia. Preliminary report research results, phase III. SRSF research report. 6. 52 pp. <http://www.mystfx.ca/research/srsf/GNSBFA/ResearchReport06.html>.
- Wilson, J., L. Yan & C. Wilson. 2007. The precursors of governance in the Maine lobster fishery. *Proc. Natl. Acad. Sci. USA* 104:15212–15217.
- Worm, B. & R. A. Myers. 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84:162–173.