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

Author(s) :Brian F. Beal and George C. Protopopescu
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OCEAN-BASED NURSERIES FOR CULTURED LOBSTER (*HOMARUS AMERICANUS* MILNE EDWARDS) POSTLARVAE: FIELD EXPERIMENTS OFF THE COAST OF EASTERN MAINE TO EXAMINE EFFECTS OF FLOW AND CONTAINER SIZE ON GROWTH AND SURVIVAL

BRIAN F. BEAL[1]* AND GEORGE C. PROTOPOPESCU[2]

[1]*University of Maine at Machias, 116 O'Brien Avenue, Machias, ME 04654;* [2]*Downeast Institute for Applied Marine Research & Education, PO Box 83, Beals, ME 04611*

ABSTRACT Historically, stock enhancement programs for American lobster, *Homarus americanus*, have a common theme: production and release of large numbers of stage IV or stage V individuals. However, these animals are difficult to mark, highly mobile when released on the bottom, and susceptible to a wide array of predators, and their claws have yet to develop bilateral asymmetry. Many of these attributes make it difficult to test the efficacy of hatch-and-release efforts. It is possible to hold postlarval lobsters individually in the laboratory or hatchery and provide food regularly for several months to release older, larger individuals (as with enhancement efforts in Europe with *Homarus gammarus*). However, the costs to do so compared with the value of commercial-size animals makes this practice cost prohibitive. Attempts to reduce costs of rearing early postlarvae to larger sizes in ocean-based nursery cages in eastern Maine for periods of longer than 1 y have resulted in variable survival (in general, <50%) and slow growth (doubling in carapace length (CL) from 4.2–8.9 mm). A series of field trials (2004 to 2010) examined methods to improve survival rates and enhance growth with the goal of producing animals large enough to apply a physical tag that can be seen easily by fishers and scientists interested in testing directly the efficacy of enhancement efforts. The effect of flow rates into and out of various types of containers (350 mL and 440 mL) holding individual, cultured stage IV lobsters was examined experimentally during a 309-day period from August 2004 to July 2005 in off-bottom, ocean-based nursery cages deployed in shallow (12 m) water near Great Wass Island, Beals, ME. Mean survival rate varied directly with flow as animals in containers with the greatest exchange of seawater demonstrated survival rates of ca. 90% compared with ca. 30% in containers allowing lower flow rates. Sediment deposition in the low-flow rate containers tended to be high, and was associated with significantly lower mean lobster survival. In a separate field trial in shallow water from August 2009 to October 2010 (419 days), lobster growth in submerged wooden trays was assessed using 5 different container sizes that ranged from 0.02–0.26 m^2 (ca. 1.5–21 L). Growth was best described by a sigmoidal function, with a strong linear component over container sizes between 0.02 m^2 and 0.13 m^2 (ca. 1.5–10 L), and no significant difference observed in mean CL of lobsters in the largest 2 container sizes. Final mean CL and mass (23.9 ± 1.4 mm and 10.7 ± 2.1 g, respectively, ±95% CI) of animals in the 2 largest containers was 57.4% and 349% greater, respectively, than animals in the smallest containers. Rearing cultured individuals of *H. americanus* to large sizes in ocean-based nursery cages may provide managers of stock enhancement programs with a more viable assessment tool than those used traditionally.

KEY WORDS: American lobster, culture, *Homarus americanus*, Maine, nursery cages, stock enhancement

INTRODUCTION

The American lobster (*Homarus americanus* Milne Edwards, 1837) fishery supports one of the most important fisheries in North America (Boudreau & Worm 2010). In the United States, where most commercial activity is concentrated in the northeast region (New Jersey to Maine (Thunberg 2007)), landings from 1999 through 2009 averaged nearly 40,000 metric tons (mt) annually, worth approximately $331 million each year in dockside revenues (National Marine Fisheries Service 2011). Recent trends in the commercial lobster catch in Maine have shown unprecedented increases (e.g., 148% between 1995 and 2010 (Maine Department of Marine Resources 2011)). In Atlantic Canada, where lobster is the most valuable seafood export, recent annual landings have averaged between 50,000–55,000 mt, with exports of $805 million reported in 2009 (Department of Fisheries and Oceans Canada 2011). No general consensus exists in the scientific community regarding the biotic/abiotic mechanisms for the upsurge in and future duration of these historic landing trends (Beal 2012). However, although lobster landings in the northern, colder waters of North America continue to increase, the opposite has occurred in areas of southern New England (Massachusetts, Connecticut, and Rhode Island), where the stock is depleted, in poor condition (Atlantic States Marine Fisheries Commission 2009), and landings have decreased by 43% during the past decade to near-record lows (National Marine Fisheries Service 2011). The large variability in landings and uncertainty about why wild stocks of *H. americanus* are behaving differently in different geographical regions of the northeast United States presents an opportunity to investigate the potential role of lobster culture should stock enhancement become a management option. In addition, cultured individuals of *Homarus* may have other uses that could diversify economically the lobster industry by creating new products for the aquarium trade (sensu Calado (2008)) or the seafood industry.

Early attempts to culture American lobsters began during the 1880s at Woods Hole, MA, with the hatching of eggs and liberating stage I larvae for stock enhancement purposes (Nicosia & Lavalli 1999). Over time, various culture techniques were developed to enhance larval survival in the hatchery that resulted in the ability to produce large numbers of postlarvae (Carlson 1954, Hughes et al. 1974, Serfling et al. 1974, Van Olst

*Corresponding author. E-mail: bbeal@maine.edu
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et al. 1977, Syslo & Hughes 1981, Chang & Conklin 1993, Beal & Chapman 2001, Fiore & Tlusty 2005). The goal of most lobster hatchery programs in North America today, and in the past, has focused on enhancing wild stocks (Aiken & Waddy 1995, Beal et al. 1998, Castro et al. 2001); however, published accounts of field tests of the efficacy of these and other enhancement efforts have been lacking primarily because of the difficulty and expense associated with the logistics of such tests (Beal et al. 2002, French McCay et al. 2003). In addition, no apparent increases in landings have occurred in the vicinity of the releases (but see Comeau and Mallet (2010)).

One commonality of all North American lobster stock enhancement programs has been to release early benthic phase (stage IV) animals because this is the most cost-effective stage to produce in the hatchery as larvae can be reared en masse (typically more than 100,000 per hatchery per year) with relatively high (ca. 50%) survival rates (Beal & Chapman 2001). Unfortunately, these lobsters are highly mobile (Castro & Cobb 2005) and may not be able to detect chemical cues of unknown food items (Daniel & Bayer 1987). Although it is possible to house, feed, and maintain these cultured animals individually in the laboratory or hatchery while they attain larger sizes, the costs associated with this additional handling and maintenance are prohibitive compared with their value on reaching the commercial fishery. In contrast, lobster stock enhancement programs in Europe using cultured individuals of *Homarus gammarus* (L.) generally produce fewer (tens of thousands per hatchery per year) larger juveniles, releasing 7–9-mo-old animals with carapace lengths (CLs) greater than 10 mm (Bannister & Addison 1998, van der Meeren et al. 1998, Wickins 1998, Schmalenbach et al. 2009, but see Browne & Mercer 1998, Benevente et al. 2010). Unlike stage IV *H. americanus*, the larger, cultured *H. gammarus* are less mobile, more easily marked (Wickins et al. 1986, Linnane & Mercer 1998, Schmalenbach et al. 2011), and are more amenable to field tests of program efficacy (Bannister et al. 1994, Addison & Bannister 1994, Agnalt et al. 1999, Agnalt et al. 2004). Tlusty et al. (2005) have argued that for stock enhancement programs involving *H. americanus* to become successful, a different strategy is required that should reflect more the focus of European efforts. Specifically, they suggest that cost-effective methods be developed to rear and release older American lobsters.

The advantage of releasing older, larger animals, a strategy that transcends enhancement programs from other crustaceans (Hamasaki & Kitada 2006, Hines et al. 2008, Johnson et al. 2008), bivalves (Cigarría & Fernández 2000, Beal & Kraus 2002, Uki 2006), sea turtles (Okuyama et al. 2010), and marine fish (Yamashita et al. 1994, Fushimi 2001, Leber et al. 2005), is that the probability of surviving to the commercial fishery increases. Field experiments using wild, tethered, early benthic phase juveniles (CL, 5–40 mm) of the American lobster (Wahle & Steneck 1992) demonstrated a dramatic increase in survival with increasing body size. Castro et al. (2001) seeded artificial reefs (10 to 40-mm stones) in Narragansett Bay, RI, with cultured, marked (microwire tags) stage V and stage VI lobsters, and recovered only 1 of 4,600 (0.02%) individuals. In addition, Castro et al. (2001) observed that hatchery-reared lobsters did not seek shelter immediately, as opposed to wild animals that did. This difference in behavior of early postlarvae may contribute to higher mortalities among lobsters that have no field experience prior to release.

During the past decade, we have examined how ocean-based nursery technology developed in Ireland for cultured individuals of *H. gammarus* (Beal et al. 2002) can be applied to hatchery-reared juveniles of *H. americanus*. Specifically, the goal has been to develop cost-effective techniques to produce large numbers of relatively large (CL, >20 mm) lobsters. Initial efforts (Beal 2012) demonstrated that cultured, stage IV lobsters held in flow-through containers in the waters off eastern Maine for ca. 450 days can survive at rates up to 68%, and can double in size in some shallow-water habitats. Here, we expand on those initial field trials, and show experimentally how water flow and container size are paramount in enhancing both growth and survival of cultured *H. americanus* juveniles.

METHODS

Cultured Lobsters

For the trials conducted from 2004 to 2005 and 2006 to 2007, lobster juveniles were cultured from broodstock collected from the waters near Great Wass Island, Beals, ME (44°27.864′ N, 67°36.996′ W) between July and August 2004 and 2006, respectively. Ovigerous females were held separately without food in 150-L aerated tanks in the shellfish production facility at the Downeast Institute for Applied Marine Research & Education (DEI; Black Duck Cove, Beals, ME; 44°28.821′ N, 67°35.957′ W) for several weeks prior to releasing stage I larvae. Seawater temperature in the tanks ranged from 14–18°C. For the trials that began in 2005, lobster juveniles were cultured from broodstock collected from the waters near Beals Island between September 2004 and October 2004. These ovigerous females were held over the winter at DEI in 150-L aerated tanks and were fed crushed, live mussels weekly. Seawater temperature in the tanks ranged from 10–13°C during this period. Females began to release stage I larvae from the middle of April through mid May. Juvenile lobsters used in 2009 were produced from broodstock collected in June 2009 and July 2009 from the waters off Cutler, ME (44°38.943′ N, 67°10.217′ W). In all years, production methods for stage IV juveniles followed those described in Beal and Chapman (2001).

Submerged Nursery Cages and Flow-Through Containers

Two different submerged nursery cage systems were used in these studies. One system is described in Beal (2012). Briefly, the cages were modified vinyl-coated wire, commercial lobster traps (91 × 50 × 45 cm, with 2.5-cm apertures) with a series of 9 equidistant, horizontal shelves made from the same wire as the cage itself. Shelves held a number of flow-through containers with a single lobster inside each. Each vinyl-coated wire nursery cage was attached to an 18.9-L bucket filled with cement and used as an anchor. A 2-m rope connected the anchor to the bottom of the nursery cage. An air-filled buoy was secured to the top of each cage so that, when deployed, cages would rise up into the water column approximately 2 m off the bottom. A surface buoy was tied to the anchor. This arrangement is similar to that used by Beal et al. (1995) to overwinter juveniles of the soft-shell clam *Mya arenaria* Linneaus, 1758. The other system was a series of commercially procured, round (diameter, 50 cm) lantern nets (Coastal Aquaculture Supply, Cranston, RI; http://www.coastalaquacultural.com; aperture, 15 mm; number of

tiers, 10) constructed of UV-resistant polyethylene material. Each lantern net was anchored to a solid cement block (40×20×20 cm) with a 2-m rope. To keep each net upright in the water column, 2 45-cm-long×20-cm-diameter Styrofoam floats were affixed to the top level of each net, and a small surface float also was attached to the topmost level so that the nets could be retrieved during high or low tide.

Six container types were used in this study: (1) 350-mL plastic soda bottles with 25 holes (diameter, 2.2 mm); (2) 350-mL plastic soda bottles with 50 holes; (3) plastic Petri dishes (150 mm in diameter × 25 mm in height, or 440 mL, with 50 holes); (4) plastic Petri dishes (similar dimensions) with an 89-mm-diameter hole cut out of both the top and bottom, which were covered with a piece of fiberglass window screening (aperture, 1.8 mm) affixed to the plastic with PVC cement; (5) "squat" plastic buckets (food grade, polypropylene, Bisphenol A-free; model 3012–3.2 L, http://www.ipl-plastics.com/12-Series.aspx) that were 19.8 cm in diameter × 15 cm tall; and (6) "tall" plastic buckets (model 3712–4.2 L) that were 17.1 cm in diameter× 19.8 cm tall. For these last 2 containers, a hole (diameter, 11.4 cm) was cut from the bottom of each and replaced with a piece of fiberglass window screening that was affixed to the remaining bottom lip using hot glue (general purpose, multitemperature glue stick; http://www.glu-stix.com). In addition, each of these last 2 container types had a polypropylene lid that when pushed down over the upper lip of the container formed a tight seal. A hole of similar diameter was cut in each lid, but instead of hot gluing a piece of window screening to fill the hole, a piece (23× 23 cm) of window screening was used to cover the top of the open container. The lid was then pushed over the rim to secure the screening. Seawater was able to flow freely in to and out of each of the 6 container types.

Experiment I: Submerged Nursery Cages (2004 to 2005)

To test the effects of flow on juvenile lobster survival and growth, 13 cages were deployed in 12 m of water at low tide near Middle Ram Island, approximately 2 km west of Great Wass Island, Beals, ME (44°29.30′ N, 67°37.77′ W) on August 26, 2004. Cages were stocked with soda bottles (25 or 50 holes) and Petri dishes (50 holes or 1 large hole). Nine containers (bottles or Petri dishes) were added to each of 8 shelves per cage ($n = 72$ lobsters per cage, 1lobster per container; $n = 936$; Table 1; CL, 3.85–5.25 mm; $\bar{x} \pm 95\%$ CI $= 4.21 \pm 0.14$ mm, $n = 29$; mean mass ± 95% CI = 0.051 ± 0.0045 g, $n = 29$). Containers on each shelf were sandwiched between 2 pieces of vinyl-coated trap wire (42×38 cm) held together with nylon cable ties. Cages were retrieved on July 1, 2005 (309 days), and each container was inspected to determine the fate of the juvenile lobsters. Vernier calipers were used to measure CL and total length (TL; distal tip of the extended claws to the distal end of telson) to the nearest 0.1 mm of a random sample of 78 live animals, and a Sartorius (Acculab VIC-612) digital balance was used to measure wet mass (to the nearest 0.01 g) of a random sample of live animals (with both chelae) from each treatment ($n = 160$).

To determine effects of container type on percent survival, analysis of variance (ANOVA) was performed on the arcsine-transformed mean survival of juvenile lobsters per level. Three linear, *a priori* contrasts were examined for container type: (1) mean survival of lobsters in bottles versus mean survival of lobsters in dishes; (2) among bottles, mean survival in bottles with 25 holes versus mean survival in bottles with 50 holes; and (3) among dishes, mean survival in dishes with holes versus mean survival in dishes with the large hole covered with window screening. These contrasts were not orthogonal (sensu Littell et al. (2002)) because the number of observations differed between treatments as a result of differential survival (see Results). To control for excessive Type I errors, an adjusted decision rule (α') was used ($\alpha' = 1 - [1 - \alpha]^{1/k}$, where k is the number of contrasts (Winer et al. 1991)). In addition, to determine whether container type affected the relationship between TL and CL, and between wet mass and CL, a regression analysis was performed, culminating in an analysis of covariance (ANCOVA). The mass–CL data required a logarithmic transformation because the addition of a quadratic term to a linear model was statistically significant in a lack-of-fit test (Snedecor & Cochran 1989). The mass–CL data proved to be explained best by a power exponential model ($Y = aX^b$).

Experiment II: Floating Nursery Trays (2004 to 2005)

From subtidal nursery cage studies conducted in 2002 and 2003 (Beal 2012), and again in 2004 (see Results), it appeared that lobster growth may be related to space afforded individuals.

TABLE 1.

The arrangement of flow-through containers according to level in each of 13 nursery cages deployed on August 26, 2004, near Middle Ram Island, Beals, ME (*level 1, topmost; level 8, bottommost) for the submerged cages used in experiment I.

Level*	Container, Cages 1–7	Container, Cages 8 and 9	Container, Cages 10 and 11	Container, Cage 12	Container, Cage 13
1	Dish-screening	Dish-screening	Dish-holes	Dish-holes	Bottles-50
2	Bottle-25	Dish-screening	Bottles-50	Bottles-50	Dish-screening
3	Dish-holes	Dish-screening	Bottles-50	Bottles-50	Bottles-50
4	Bottle-50	Dish-screening	Bottles-50	Bottles-50	Dish-holes
5	Dish-screening	Dish-screening	Bottles-50	Dish-holes	Bottles-50
6	Bottle-50	Dish-screening	Bottles-50	Bottles-50	Dish-screening
7	Dish-holes	Dish-screening	Bottles-50	Bottles-50	Dish-holes
8	Dish-screening	Dish-screening	Dish-holes	Dish-screening	Dish-screening

Container type: Bottle-25 or Bottle-50 (350-mL plastic soda bottles containing 25 holes or 50 holes, respectively, that were 2.2 mm in diameter); Dish-holes or Dish-screening (440-mL Petri dish with 50 holes or with an 89-mm circular hole cut in both the top and bottom portion of the dish and covered with a piece of fiberglass window screening affixed to the dish with PVC cement, respectively). Nine containers were arrayed on each level (horizontal shelves) within each nursery cage ($n = 936$ lobsters).

Therefore, a manipulative experiment was performed to examine the relationship between fate and lobster growth rate versus the size of container in which the juvenile lobsters were held. The experiment was conducted in Mud Hole Cove (MHC), Beals, ME (44°29.13′ N, 67°35.16′ W, see Beal et al. (1995) for a description of this location). Floating wooden trays (125 × 90 × 8 cm deep) completely lined with fiberglass window screening were used to hold juvenile lobsters. Each tray was divided into 10 compartments of varying sizes. Two replicates of each of 5 sizes were used: 21.5 × 9 cm (0.0194 m^2, 1.55 L; extrasmall (XS)), 21.5 × 17.5 cm (0.03763 m^2, 3.01 L; small (S)), 28 × 22 cm (0.0616 m^2, 4.93 L; medium (M)), 45 × 28 cm (0.126 m^2, 10.08 L; large (L)), and 58.5 × 45 cm (0.2633 m^2, 21.06 L; extralarge (XL)). On September 2, 2004, each compartment in 32 trays was stocked with a stage IV lobster ($n = 320$; mean CL ± 95% CI = 4.38 ± 0.25 mm, $n = 19$). The top of each tray was covered with a piece of thin, black plastic sheeting to deter sea gull (*Larus argentatus* Pontoppidan, 1763, and *Larus marinus* Linneaus, 1758) predation on the lobsters inside. Floating trays were stored temporarily in 1 of 2 commercial lobster impoundments at Black Duck Cove, and were deployed at MHC the following day. Each compartment of one half of the trays ($n = 16$) received 4 plastic Bio-Spheres biofouling balls (diameter, 5 cm; http://www.fishfarmsupply.ca) in an attempt to test whether the additional surface area provided by the balls would enhance fouling material and provide additional food resources for the cultured lobsters. The remaining 16 trays served as controls without biofouling balls. On January 3, 2005 (154 days), trays were recovered from MHC and returned to DEI. The CL of each live lobster was measured to the nearest 0.01 mm using a dissecting microscope with ocular micrometer, TL was measured to the nearest 0.1 mm using Vernier calipers, and the mass of each was recorded to the nearest 0.01 g using a Sartorius digital balance. ANOVA was performed on the untransformed mean survival of lobsters and their mean mass. The linear model included the 2 main factors that were orthogonal to each other: biofouling spheres and compartment size. A series of 4 planned contrasts was examined to understand more fully the effect of compartment size on each dependent variable: $\bar{x}_{XL}$ versus $\bar{x}_{Rest}$; $\bar{x}_L$ versus $\bar{x}_{M,\ S,\ XS}$; $\bar{x}_M$ versus $\bar{x}_{S,\ XS}$; and, $\bar{x}_S$ versus $\bar{x}_{XS}$. An adjusted decision rule (α') of 0.0127 was used (Winer et al. 1991). An analysis of regression lines (i.e., test for slope equality) and subsequent ANCOVA were performed to examine effects of the presence of biofouling balls and compartment size on the relationship between wet mass and CL.

Experiment III: Floating Nursery Trays (2005)

Because of the short duration of experiment II and the relatively high survival rates in the floating trays (see Results), a second test of container size on lobster growth and survival was initiated in spring 2005 using floating trays with the same array of 10 compartment sizes (as described in the previous section). On May 28, 2005, a cultured lobster (mean CL ± 95% CI = 3.91 ± 0.1 mm, $n = 15$) was added to each of the 10 compartments in 16 wooden trays deployed at MHC (as described earlier). On June 8, 2005, an additional 16 floating wooden trays were deployed at MHC with 10 lobsters each. Trays deployed in June contained larger animals (mean CL = 9.3 ± 0.43 mm, $n = 16$) that had been reared during 2004 and kept at DEI over the winter. All 32 trays were collected on November 19, 2005 (175 days or 164 days), and taken to DEI, where each was inspected for live animals.

Experiment IV: Lantern Nets (2006 to 2007)

As a result of the massive mortality in the floating trays during fall 2005 (see Results), an additional test to examine the effect of container size on fate and growth of cultured lobsters was performed using commercial lantern nets ($n = 9$) as nursery cages. This trial was conducted from August 2, 2006, to November 19, 2007 (474 days), at MHC. The 2 bottommost tiers of each lantern net were not used in this trial. In tiers 1 (top) and 8 (bottom), a single cultured lobster juvenile was added to each of 3 Petri dishes with 89-mm holes covered with fiberglass window screening (as described earlier). Dishes were sandwiched between 2 pieces of vinyl-coated lobster trap wire (48 cm long × 20 cm wide) that were cinched together using nylon cable ties. Cultured lobsters were added to tall buckets on tiers 2, 4, and 6. Two of the 4 buckets on each tier contained a coarsely crushed shell (*M. arenaria*) substrate (air-dried for more than 1 y, and to a depth of 3 cm within each bucket) that originated from a local commercial clam shucking shop. The other 2 buckets contained no substrate; lobsters encountered only the window screening material on the bottom of those buckets. Squat buckets were placed on tiers 3, 5, and 7. As with the tall buckets, 2 of the squat buckets on each tier contained shell substrate, and 2 did not. The polyethylene material comprising the bottom of each tier of the lantern net was sufficient to support the 4 buckets. Nets were deployed in 5 m of water at low tide. At the end of the experiment, the CL and wet mass of all live animals was measured (as described earlier).

ANOVA was performed on the untransformed mean percent survival data (November 19, 2007) and mean final CL using the following linear model:

$$Y_{ijklm} = \mu + A_i + B_j + AB_{ij} + C(B)_{k(j)} + AC(B)_{ik(j)} + D(CB)_{l(jk)} + AD(CB)_{il(jk)} + e_{m(ijkl)}$$

where Y_{ijklm} is the dependent variable (percent survival, CL), μ is the theoretical mean, A_i is net (where i is 9 lantern nets; factor is random), B_j is the container (where j is 3 sizes: dish, squat bucket, or tall bucket; factor is fixed), C_k is the tier (where $k = 2$ (for dishes) or $k = 3$ (for buckets); factor is fixed), D_l is the substrate (where $l = 2$ – crushed shell versus no shell; factor is fixed), and e_m is experimental error. Analysis of the regression lines and ANCOVA were performed on the ln-transformed wet mass versus CL to examine effects of container size and substrate.

Experiment V: Submerged Nursery Trays (2009 to 2010)

Because the catastrophic lobster losses observed in experiment III appeared related to a large rainfall event in fall 2005 (see Results), another attempt was made to determine whether the wide range of container sizes incorporated into the experimental design of the floating tray study would affect survival and growth of small, cultured lobsters. Twelve wooden trays with 10 compartments each (as described earlier) were deployed at MHC on August 12, 2009; however, in this experiment each tray was submerged separately, remaining approximately 1.5 m off the bottom until the experiment was terminated on October

5, 2010 (419 days). Trays were submerged by placing a 1.5-m rope bridle at each corner, then tying all 4 bridles together underneath each tray, and attaching it to a cement block (25 × 20 × 20 cm) filled with cement. One half of the trays was lined completely with fiberglass window screening (aperture, 1.8 mm, as described earlier), and the other half was lined with a synthetic nylon screen (Nitex; aperture, 2 mm). Mean CL ± 95% CI for juveniles used in this trial was 3.9 ± 0.12 mm ($n = 44$). Number of lobsters alive at the end of the trial was counted, and the CL, TL, and mass of all live animals were measured at the end of the experiment (as described earlier).

ANOVA was performed on the mean number of surviving lobsters as well as mean CL using the following linear model:

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

where Y_{ijkl} is the dependent variable (number alive, CL), μ is the theoretical mean, A_i is the mesh (where i is 2 sizes: 1.8-mm aperture vs. 2-mm aperture; factor is fixed), B_j is the container size (where j is 5 sizes: 0.0194 m^2 (XS), 0.0376 m^2 (S), 0.0616 m^2 (M), 0.1260 m^2 (L), or 0.2633 (XL) m^2; factor is fixed), C_k is the tray (where $k = 6$ for each mesh size; factor is random), and e_l is the experimental error.

Four planned contrasts were performed to understand more completely the effects of compartment size on each dependent variable: (1) $\bar{x}_{L\ \&\ XL}$ versus $\bar{x}_{Rest}$, (2) $\bar{x}_L$ versus $\bar{x}_{XL}$, (3) $\bar{x}_{XS}$ versus $\bar{x}_{S\ \&\ M}$, and (4) $\bar{x}_S$ versus $\bar{x}_M$. An adjusted decision rule (α') of 0.0127 was used (Winer et al. 1991). Analysis of regression lines followed by ANCOVA was performed on the ln-transformed mass-versus-CL data to examine how mesh size and compartment size influence this relationship. Animals that had molted recently (color of exoskeleton was bright red, and mass was noticeably lower for a given CL), and those missing one or more chelae, were not included in the regression analysis.

Experiment VI: Communal Rearing (2005)

To determine whether communal rearing is a viable alternative to rearing juvenile lobsters in separate ocean-based containers, we initiated an experiment on September 14, 2005, in a flow-through cement tank (28,000 L) at DEI. Five round piles (each approximately 0.75 m in diameter × 0.18 m tall) of dried, crushed blue mussel (*Mytilus edulis* Linnaeus, 1758) shells were assembled and placed equidistant from each other on the bottom of the tank. The tank was filled gradually (over 1.5 h) with ambient seawater to a depth of 0.15 m, and 50 stage IV lobsters were distributed haphazardly to the shells in each pile as the seawater began to inundate each pile. The tank was then filled to capacity, and ambient, unfiltered seawater continued to flow into this tank throughout the duration of the test. A standpipe covered with a piece of fiberglass window screening allowed seawater to exit the tank. On November 4, 2005, after 51 days, the water was slowly drained from the tank, the contents of each pile was sieved carefully using a 2-mm mesh, and all live lobsters were counted.

RESULTS

Experiment I: Submerged Nursery Cages (2004 to 2005)

Twelve of the 13 cages deployed on August 26, 2004, were recovered on July 1, 2005. Cage 7 (Table 1) was not found. Mean percent survival varied considerably among cages (minimum, 23.6%; maximum, 88.8%); however, differences in container type and level in cages explained most of this variability. For cages 1–6 (Table 1), highest mean survival of juvenile lobsters (91.7 ± 5.3%, $n = 18$; 3 cages × 3 levels per cage) was observed in Petri dishes with screening and Petri dishes with holes (74.9 ± 8.6%, $n = 12$; Table 2). Lowest mean survival occurred in bottles (31.2 ± 15.7%, $n = 18$; Fig. 1). ANOVA with preplanned contrasts (Table 3) demonstrated highly significant differences in mean percent survival between dishes and bottles ($P < 0.0001$), between dishes with holes and dishes with screening ($P < 0.0034$), but not between bottles with 25 holes versus 50 holes ($P = 0.6897$).

Juvenile lobsters in cages 8 and 9 (Table 1) had 2 of the 3 highest overall survival rates (cage 8, 88.8%; cage 9, 86.6%). Because containers on all levels of both cages were identical (Petri dishes with screening), a test was conducted to determine whether mean survival differed between the 4 upper (82.6 ± 10.1%, $n = 8$) and 4 lower levels (92.7 ± 9.2%, $n = 8$). ANOVA demonstrated these means to be significantly different ($P = 0.0412$, Table 4, Fig. 2).

The greatest difference in juvenile lobster survival between 2 cages with a similar arrangement of containers from level to level occurred in cages 10 and 11 (23.6% vs. 66.3%, Table 1, Fig. 3). Because variances were excessive, ANOVA was unable to detect a significant difference in mean survival between the 2 cages ($P = 0.0726$). Similarly, lobster survival in Petri dishes with 50 holes was ca. 100% greater than that observed in bottles with 50 holes (72.7 ± 23.3% ($n = 4$) vs. 35.7 ± 22.6% ($n = 12$), respectively); however, this difference also was not statistically significant ($P = 0.0671$).

Mean lobster survival in cages 12 and 13 (Table 1) was highly variable (46.4% vs. 71.4%, respectively); however, survivorship in both demonstrated trends similar to those observed in cages 1–6—that is, significantly higher survival in Petri dishes (pooled across types, 87.5 ± 5.9%, $n = 8$) than in bottles (30.4 ± 17.0%, $n = 8$; $P = 0.0002$, Fig. 4).

The relationship between TL and CL was linear and was unaffected by the type of container in which the lobsters were

TABLE 2.

Mean survival (± 95% CI) of juvenile lobsters held in flow-through containers from cages 1–6 (see footnote in Table 1) from August 26, 2004, to July 1, 2005 (309 days), near Middle Ram Island, Beals, ME.

Level	Container	% Survival (95% CI)	% Survival Minimum	% Survival Maximum
1	Petri dishes with screen	92.6 (9.5)	77.8	100.0
2	Bottles with 25 holes	30.9 (34.6)	0.0	80.9
3	Petri dishes with 50 holes	77.8 (12.8)	55.6	88.9
4	Bottles with 50 holes	31.7 (37.8)	4.8	100.0
5	Petri dishes with screen	96.1 (6.5)	87.5	100.0
6	Bottles with 50 holes	30.9 (33.3)	0.0	90.5
7	Petri dishes with 50 holes	72.2 (16.1)	44.4	88.8
8	Petri dishes with screen	86.3 (15.1)	62.5	100.0

Level 1, topmost shelf of each cage; level 8, bottommost shelf of each cage. Container types are described in Methods and footnote to Table 1. $n = 6$.

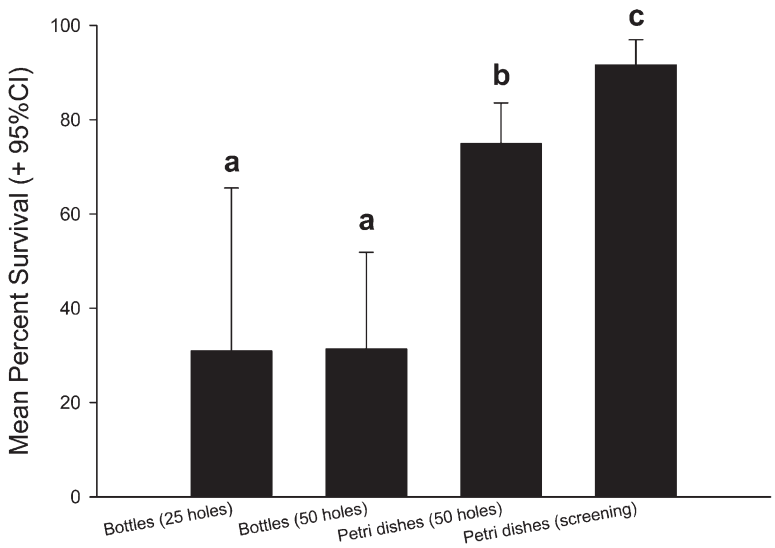

Figure 1. Mean percent survival + 95% CI of stage IV lobsters held in cages 1–6 (Table 1) deployed 2 m off the bottom from August 26, 2004, to July 1, 2005 (309 days), near Middle Ram Island, Beals, ME. $n = 6$ and $n = 12$ for bottles with 25 holes and 50 holes, respectively. $n = 12$ and $n = 18$ for Petri dishes with 50 holes and window screening, respectively. Letters above each bar that are similar indicate equal means.

held (Fig. 5). Mean CL and TL was 33.7% and 37.9% greater, respectively, for lobsters held in Petri dishes versus bottles ($P < 0.0001$, Table 5). Maximum CL and TL was 9.6 mm and 38.2 mm, respectively, in the dishes compared with 7.4 mm and 28.2 mm, respectively, in the bottles. The relationship between wet mass and CL was allometric (Fig. 6), and the ln-transformed lines were parallel ($P = 0.9076$); however, ANCOVA demonstrated that the adjusted mean mass was significantly heavier for a given CL for animals residing in the dishes compared with those in the bottles ($P = 0.0016$). Unadjusted mean wet mass was 143.9% greater in dishes (0.30 ± 0.02 g, $n = 136$) than in bottles (0.12 ± 0.02 g, $n = 24$; $P < 0.0001$, Table 6). In addition, lobsters reared in dishes with screening (0.33 ± 0.02 g, $n = 102$) were 60.7% heavier than those reared in dishes with holes (0.21 ± 0.02 g, $n = 34$; Table 6, Fig. 7).

Experiment II: Floating Nursery Trays (2004 to 2005)

Mean lobster survival in the 32 floating trays from September 2004 to January 2005 was $80.6 \pm 6.2\%$. Neither the presence of biofouling balls nor the size of the compartment had a significant effect on mean survival (Table 7). Significant variation in survival occurred between trays in the same biofouling treatment ($P = 0.0048$, Table 7). Neither compartment size (Fig. 8) nor the presence of the biofouling balls had a significant effect on the relationship between wet mass and CL. Mean wet mass was 21.6% greater for lobsters in the largest compartments versus the pooled mean of the others (Table 8, $P = 0.0037$; Fig. 9). Of the 258 surviving animals, 42 (16.3%) either had both chelae missing or a single chelae. Chelae number (0, 1, or 2) at the end of the trial was independent of the presence of biofouling balls ($G = 0.8465$, $df = 2$, $P = 0.6549$).

TABLE 3.

Analysis of variance on the arcsine-transformed mean percent survival per level of juvenile lobsters contained in cages 1–6 (see Table 1).

Source of Variation	*df*	SS	MS	F	Pr > F
Cage	5	5,240.86	1,048.17	No test	—
Level	7	19,952.34	2,850.33	12.64	**<0.0001**
Petri dishes vs. bottles	1	17,252.32	17,252.32	76.52	**<0.0001**
Petri dish (hole vs. screen)	1	2,227.63	2,227.63	9.88	**0.0034**
Bottles (25 holes vs. 50 holes)	1	36.54	36.54	0.16	0.6897
Cage × Level = Error	35	7,890.73	225.45		
Total	47	33,083.93			

Nine containers were arrayed on each of 8 shelves per cage. Seven cages were deployed near Middle Ram Island, Beals, ME, on August 26, 2004, and 6 cages were retrieved on July 1, 2005. Cages (random factor) were suspended 2 m off the bottom using an arrangement of floats and anchors (see Methods). An adjusted decision rule (α') of 0.0169 was used for the set of 3 *a priori* contrasts associated with the level source of variation (fixed factor). *P* values in bold type indicate statistical significance.

TABLE 4.

Analysis of variance on the arcsine-transformed mean percent survival per level of juvenile lobsters in cages 8 and 9 (Table 1).

Source of Variation	*df*	SS	MS	F	Pr > F
Level	7	1,681.67	240.24	2.62	0.1000
Top 4 vs. bottom 4	1	540.58	540.58	5.90	**0.0412**
Error	8	732.48	91.56		
Total	15	2,414.15			

Both cages were deployed near Middle Ram Island, Beals, ME on August 26, 2004, and were retrieved 309 days later on July 1, 2005. Cages were suspended 2 m off the bottom using an arrangement of floats and anchors (see Methods). A single degree-of-freedom contrast was used to test for differences in mean lobster survival between the top 4 levels versus the bottom four levels. *P* values in bold type indicate statistical significance.

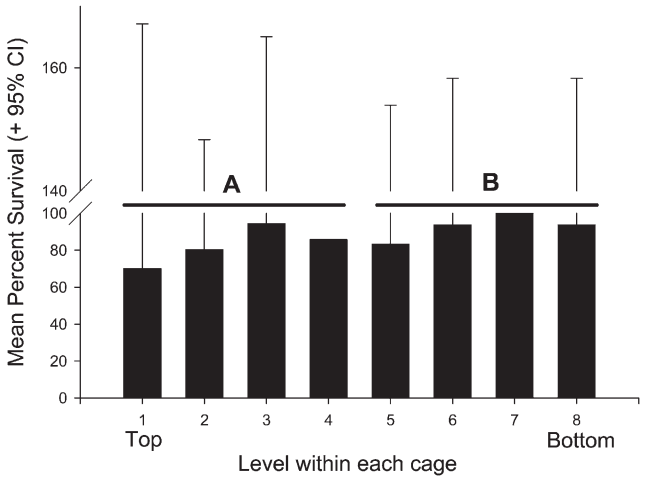

Figure 2. Mean percent survival + 95% CI of stage IV lobsters held in cages 8 and 9 (Table 1) deployed 2 m off the bottom near Middle Ram Island, Beals, ME, from August 26, 2004, to July 1, 2005 (309 days). Lobsters were held singly in 440-mL Petri dishes with an 89-mm hole cut into both the top lid and bottom that was covered with fiberglass window screening. Different letters above the bars indicate statistically significant grouping. $n = 2$.

Experiment III: Floating Nursery Trays (2005)

No lobsters survived in any of the floating nursery cages. When cages were examined in November, dead, brittle shell was discovered in many of the compartments. Several pieces indicated that CLs were as large as 15–20 mm, but that death had occurred many weeks prior to the sampling. Because trays were floating, it is possible that heavy rainfall events that occurred in mid October along the eastern Maine coast were responsible for the mortality.

Experiment IV: Lantern Nets (2006 to 2007)

Survival in the lantern nets was low (24.1 ± 6.1% in November 2007, $n = 9$). All nets had become heavily fouled with macroalgae (*Laminaria longicruris* Bachelot de la Pylaie), and many were resting on the bottom. None of the mesh screening on any experimental units was ripped or torn; however, more than 50% were filled with soft mud. It is unknown whether the mud contributed to lobster mortality or appeared after the lobsters died. Most of the containers with live lobsters, independent of container size, had little or no mud, indicating active movement of the animal inside. Mean CL of live lobsters in the 9 nets in November 2007 was 12.6 ± 0.5 mm ($n = 65$).

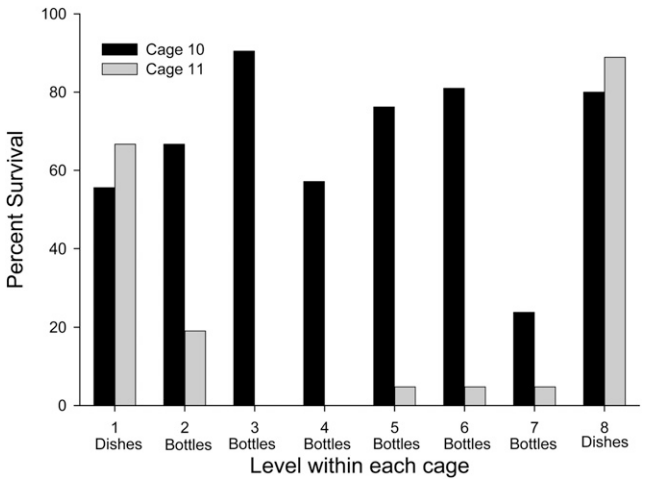

Figure 3. Percent survival of stage IV lobsters held in 2 cages (10 and 11, Table 1) deployed 2 m off the bottom near Middle Ram Island, Beals, ME, from August 26, 2004, to July 1, 2005. Mean survival ± 95% CI in Petri dishes (50 holes) and bottles (50 holes) pooled across both cages was 72.7 ± 23.3% ($n = 4$) and 35.7 ± 22.6% ($n = 12$), respectively ($P = 0.0671$). Level 1, top; level 8, bottom.

No significant variability in lobster survival was observed between nets ($P = 0.3662$), nor was there an overall effect resulting from type of container ($P = 0.9802$); however, the effect of container type varied significantly from net to net ($P = 0.0212$, Table 9). Separate 1-way ANOVAs were performed to examine this interaction source of variation further; however, no pattern was revealed. For example, container type was a statistically significant source of variation for 3 of the 9 nets, but none of the tests had similar results (net A, survival in the dishes was greater than the combined mean of the squat and tall buckets (66.7% vs. 12.5%); net B, survival in squat buckets was less than in tall buckets (8.3% vs. 50%); net C, survival in squat buckets was greater than in tall buckets (41.7% vs. 8.3%)). Lobster survival was approximately 20% greater in buckets with shell versus those without (25.9 ± 8.3% vs. 21.2 ± 7.8%, $n = 108$).

Container type had a significant effect ($P = 0.0011$) on mean CL (Table 10). Lobsters were 33% larger in buckets regardless of substrate (13.3 ± 0.52 mm, $n = 51$) compared with those in Petri dishes (10.0 ± 0.53, $n = 14$). Analysis of regression lines (ln-transformed wet mass vs. CL) demonstrated that the slopes of the lines were similar ($F = 1.04$, $df = 1, 55$, $P = 0.3116$), and ANCOVA revealed no significant effect resulting from either container size ($F = 2.06$, $df = 2, 60$, $P = 0.1360$) or substrate ($F = 3.05$, $df = 1, 60$, $P = 0.0859$).

Experiment V: Submerged Nursery Trays (2009 to 2010)

Only 10 of the 12 wooden trays were recovered on October 5. Two of the trays lined with window screening had 2 holes each, and all 4 holes were much larger than any of the live lobsters; therefore, information from these 6 compartments was eliminated from subsequent analyses. Most trays had large quantities of mud in the compartments that likely helped contribute to some of the mortality. Survival varied significantly with mesh size ($P = 0.0264$, Table 11A), as nearly 50% more lobsters survived in submerged trays lined with the 2-mm nylon mesh than those with the 1.8-mm fiberglass mesh (74.0 ± 12.6% ($n = 50$) vs. 50.0 ± 15.1% ($n = 46$), respectively). Compartment size did not play a significant role in lobster survival ($P = 0.9526$, Table 11A).

Final mean lobster size (CL) did not vary significantly with size of mesh, but increased dramatically with increasing compartment size ($P < 0.0001$, Table 11B, Fig. 10). ANOVA and the preplanned contrasts suggested that CL increases as a step function with compartment size; however, the highest percent of variation in CL explained by container size occurred using a 3-parameter sigmoid function (SigmaPlot 11; $r^2 = 0.6768$, Fig. 10). When data from the largest container size was excluded, a lack-of-fit test indicated a strong linear relationship between CL and container size ($F = 119.64$, $df = 1, 48$, $r^2 = 0.71$, $P < 0.001$), with no significant quadratic or cubic component ($P > 0.30$). The planned contrasts between the 2 largest compartment sizes (L vs. XL) demonstrated no significant difference in mean

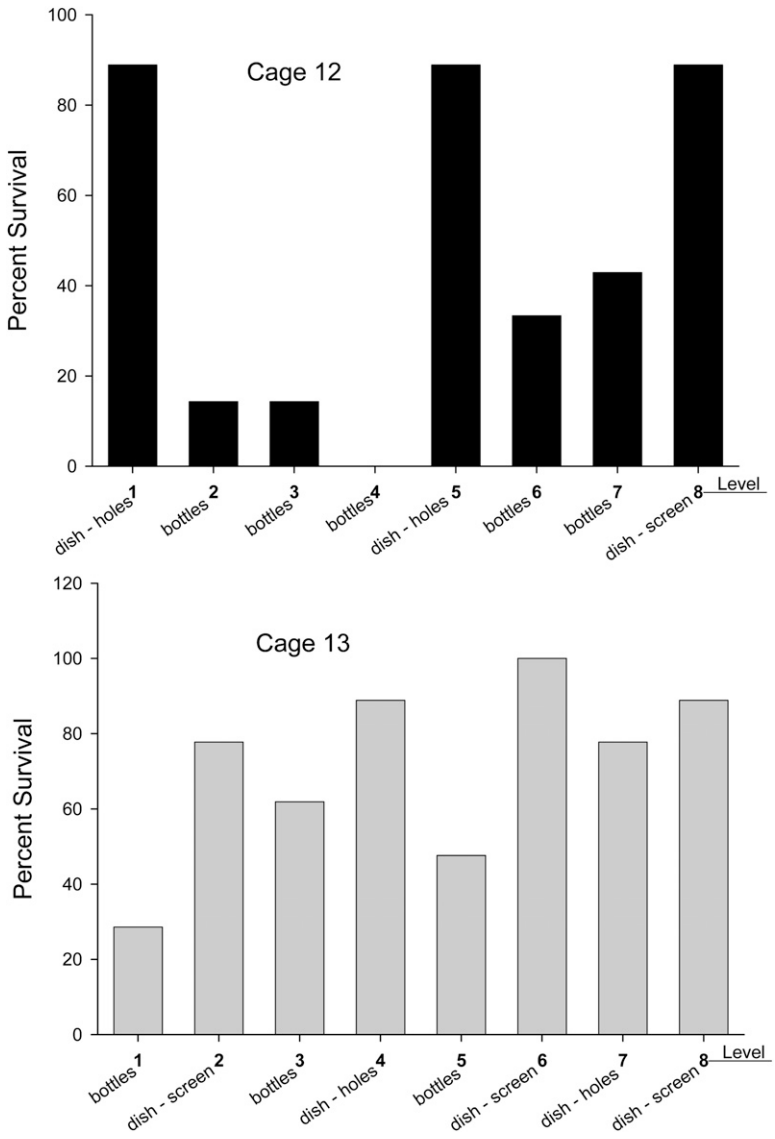

Figure 4. Percent survival of stage IV lobsters held in 2 cages (12 and 13, Table 1) deployed 2 m off the bottom near Middle Ram Island, Beals, ME, from August 26, 2004, to July 1, 2005. Significant differences in the arcsine-transformed survival percentages occurred between container types when the pooled means from each cage were compared ($P = 0.0002$). Planned contrasts demonstrated significant differences in mean survival between bottles (50 holes: 30.4 ± 17.0%, $n = 8$) and dishes (pooled across type: 87.5 ± 5.9%, $n = 8$). Level 1, top; level 8, bottom.

CL (0.126 m^2 (23.5 ± 1.49 mm, $n = 13$) and 0.263 m^2 (24.3 ± 2.9 mm, $n = 10$), $P = 0.4215$; Table 11B). The CL and TL of the largest lobster was 31.2 mm and 131.1 mm, respectively, with that individual growing in the largest compartment. Conversely, the smallest lobster was found growing in the smallest compartment (0.019 m^2), with a CL and TL of 12.5 mm and 48.0 mm, respectively. The relationship between wet mass and CL was best explained by an allometric function. The 5 ln-transformed regression lines (Fig. 11) were parallel ($F = 0.50$, $df = 4, 50$, $P = 0.7331$), and ANCOVA showed that compartment size had no effect on this relationship ($F = 0.39$, $df = 4, 54$, $P = 0.8160$).

Experiment VI: Communal Rearing (2005)

Seawater temperatures ranged from a high of 13°C on September 14 to a low of 10°C on November 3. Mean survival of the 50 lobsters distributed in each of the 5 piles of mussel shells was 2.8 ± 3.8% (range, 0–8%). No live lobsters were found outside any of the piles on the bottom of the tank, and none was observed on the screening covering the standpipe at any time during the experiment.

DISCUSSION

The results presented here provide further evidence that postlarvae of *H. americanus* can survive and grow inside flow-through containers placed in the ocean for periods over a year, and offer plausible mechanisms for reduced growth and poor survival observed in previous studies with hatchery-reared conspecifics (Beal 2012) and congeners (Beal et al. 2002).

Survival

Survival of lobsters in Petri dishes held at relatively shallow depths in off-bottom, submerged cages for ca. 300 days (2004 to

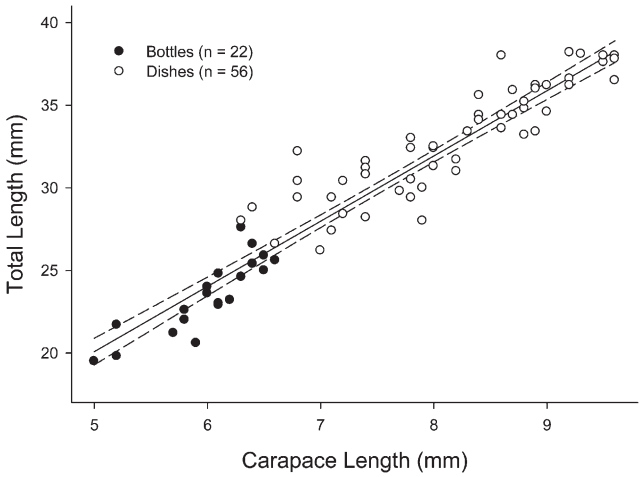

Figure 5. Relationship between final total length (TL) and final carapace length (CL) of cultured lobsters inside flow-through containers (350-mL bottles or 440-mL Petri dishes). Containers were placed inside wire cages and deployed 2 m off the bottom near Middle Ram Island, Beals, ME, from August 26, 2004, to July 1, 2005. Analysis of covariance indicated that the relationship was unaffected by container types ($P = 0.0860$). Pooled equation: $Y = 0.344 + 3.948X$ ($r^2 = 0.912$, $n = 78$, $P < 0.0001$). Dotted line represents the 95% CI. ANOVA indicated that mean CL and TL varied significantly across container type (see Table 5).

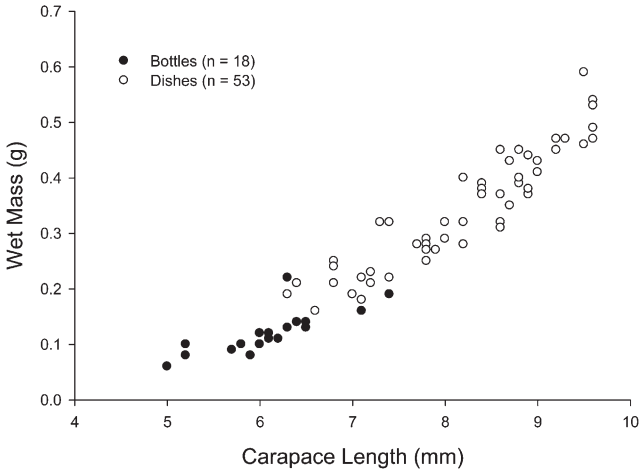

Figure 6. Relationship between wet mass and carapace length (CL) of cultured lobsters inside flow-through containers (350-mL bottles or 440-mL Petri dishes). Containers were placed inside wire cages and deployed 2 m off the bottom near Middle Ram Island, Beals, ME, from August 26, 2004, to July 1, 2005. ANCOVA on the ln-transformed data indicated that the adjusted mean mass was significantly heavier for a given CL for lobsters held in dishes versus bottles ($P = 0.0016$).

2005) averaged 75% in dishes with 50 small holes (2.2-mm diameter) compared with 91.7% in dishes with a large (89-mm) hole covered with fiberglass screening (1.8-mm-diameter aperture; Table 2, Fig. 1). Although flow rate in each container type was not measured directly, observations of their sinking rate were made in a tank of seawater. Dishes with 50 holes took up to 10 sec to fill and sink, whereas those with the large, screen-filled hole took less than 2 sec to sink. Beal (2012) used small, plastic soda bottles with 10–15 holes (2.2-mm diameter) to house cultured stage IV lobsters in submerged nursery cages in waters off eastern Maine (2002 to 2003). Most tended to fill with muddy sediments, and lobster survival was poor (<0.2%, only 1 of 630 1obsters survived for 317–357 days). In the current study, stage IV lobsters were added to similar-size plastic bottles, but the number of holes per bottle was increased to 25 or 50. No significant difference in survival was observed between these 2 treatments, and survival was greater (ca. 30%; Figs. 1 and 4) than that observed by Beal (2012); however, these rates were low compared with those observed in Petri dishes with a similar number of holes or with the window screening covering the large hole. Because dishes were approximately 25% greater in volume than bottles (440 mL vs. 350 mL, respectively), it is

TABLE 5

Analysis of variance on the untransformed mean carapace length (A) and total length (B) of 78 randomly selected cultured lobsters from all 12 nursery cages recovered on July 1, 2005, after 309 days within flow-through containers (350-mL plastic bottles and 440-mL Petri dishes; see description in Methods).

(A)

Source of Variation	*df*	SS	MS	F	Pr > F
Container	3	69.88	23.29	34.42	**<0.0001**
Bottles vs. Petri dishes	1	11.63	11.63	17.18	**<0.0001**
Bottles (25 holes vs. 50 holes)	1	0.02	0.02	0.02	0.8790
Dishes (holes vs. screen)	1	2.23	2.23	3.30	0.0734
Error	74	50.09	0.68		
Total	77	119.97			

(B)

Source of Variation	*df*	SS	MS	F	Pr > F
Container	3	1,325.24	441.75	45.07	**<0.0001**
Bottles vs. Petri dishes	1	247.98	247.98	25.30	**<0.0001**
Bottles (25 holes vs. 50 holes)	1	0.05	0.05	0.00	0.9452
Dishes (holes vs. screen)	1	33.45	33.45	3.41	0.0687
Error	74	725.32	9.80		
Total	77	2,050.56			

Containers were held in wire cages situated 2 m above the bottom near Middle Ram Island, Beals, ME. To control for excessive Type I errors, *a priori* contrasts use an adjusted decision rule (α') of 0.0169. *P* values in bold type indicate statistical significance.

TABLE 6.

Analysis of variance results on the untransformed mean wet mass (in grams) of cultured lobsters on July 1, 2005, 309 days after adding stage IV animals to flow-through containers placed 2 m off the bottom near Middle Ram Island, Beals, ME.

Source of Variation	*df*	SS	MS	F	Pr > F
Container	3	0.994	0.349	43.24	**<0.0001**
Bottles vs. Petri dishes	1	0.336	0.336	43.85	**<0.0001**
Bottles (25 holes vs. 50 holes)	1	0.000	0.000	0.04	0.8510
Dishes (holes vs. screen)	1	0.375	0.375	48.96	**<0.0001**
Error	156	1.195	0.008		
Total	159	2.189			

Animals were similar in size and mass at the beginning of the trial. The 3 *a priori* contrasts use an adjusted decision rule (α') of 0.0169. *P* values in bold type indicate statistical significance.

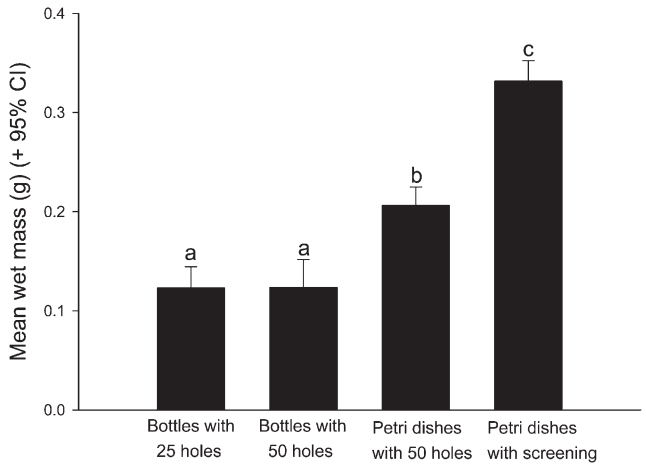

Figure 7. Mean wet mass (+95% CI) of cultured lobsters inside 4 types of flow-through containers (350-mL bottles with 25 or 50 2.2-mm holes; 440-mL Petri dishes with a total of 50 holes or window screening covering an 89-mm-diameter hole in both the top and bottom portion). Data were collected on July 1, 2005, after lobsters had been in containers for 309 days at 2 m off the bottom near Middle Ram Island, Beals, ME. Means with similar letters indicate equality ($P > 0.05$). $n_{\text{bottles with 25 holes}} = 7$, $n_{\text{bottles with 50 holes}} = 17$, $n_{\text{dishes with 50 holes}} = 34$, $n_{\text{dishes with screening}} = 102$.

unclear whether the observed difference in lobster survival (Table 3) was the result of size/volume differences between the 2 container types or container configuration.

The importance of flow into and out of containers on survival of cultured *H. americanus* juveniles is underscored on further examination of data from Beal (2012). In that study, 2 groups of 5 Petri dishes (with 10–15 2.2-mm holes drilled in each) were stacked on top of each other, and the 10 dishes added to shelves in nursery cages similar to those used in experiment I (see Methods) of the current study. The cages were deployed at several shallow-water sites in eastern Maine for 448 days during 2002 and 2003. At the end of the trial, overall mean lobster survival was 130% greater in the upper dishes versus the lower dishes in the stacks. Closer inspection of the dishes at each level in the cages showed that most in the upper stack were clean and lacked much sediment. Conversely, dishes in the lower stack, which presumably received less flow, were filled with muddy sediments and contained significantly fewer live lobsters. In the current study, lobster survival was ca. 50% greater in submerged nursery trays lined completely with 2-mm screening versus 1.8-mm window screening. Presumably, lower flow rates contribute to increased sediment deposition in containers regardless of their size and configuration. Wild juveniles of *H. americanus* are known to inhabit soft muds (Berrill & Stewart 1973), but are more abundant on cobble–boulder habitats (Wahle & Steneck 1991). Sediment deposition into bottles, dishes, buckets, and submerged nursery trays may have been too fast, creating anoxic conditions or clogging the gills, and limiting oxygen exchange. In addition, muddy conditions in flow-through containers could decrease food availability by reducing the area for organisms requiring hard substrates to settle (but see Knudsen and Tveite (1999)). Enhancing flow and reducing sedimentation may improve the quantity, and perhaps quality, of planktonic food that becomes available to the contained lobsters, and may lead to a higher biomass of fouling organisms that require relatively clean, hard surfaces and an abundant supply of floating phytoplankton or zooplankton to survive and grow.

Other factors, such as freshwater from storms and runoff from land presumably reduce lobster survival in floating nursery trays. For example, the 2005 floating tray experiment yielded no live lobsters, and it appeared that heavy rain events during that fall might have played a role in this outcome. Several small streams drain into MHC, and it is possible that with the rain that occurred day after day from tropical storms in mid October 2005, a lens of freshwater developed in the area of the cove where lobster trays were floating. Exposure to salinities less than 12 psu for 48 h is lethal for juveniles held at 15°C (McLeese 1956). Caution should be used in the future if floating nursery trays are used for juvenile lobster grow-out.

TABLE 7.

Analysis of variance on the mean number of lobsters in floating trays in Mud Hole Cove, Beals, ME, on January 3, 2005.

Source of Variation	*df*	SS	MS	F	Pr > F
Bio-Spheres (present vs. absent)	1	0.546	0.546	1.88	0.1810
Compartment	4	0.240	0.006	0.21	0.9332
XL vs. L, M, S, XS	1	0.225	0.225	0.77	0.3861
L vs. M, S, XS	1	0.001	0.001	0.00	0.9503
M vs. S, XS	1	0.005	0.005	0.02	0.9018
S vs. XS	1	0.009	0.009	0.03	0.8627
Bio-Spheres × compartments	4	0.077	0.019	0.07	0.9915
Tray (Bio-Spheres)	30	8.726	0.291	1.88	**0.0048**
Error	280	43.385	0.155		
Total	319	52.972			

Stage IV lobsters were placed into trays on September 2, 2004. Each of 32 trays contained 2 replicates of 5 compartment sizes (extrasmall (XS), 0.019 m^2; small (S), 0.038 m^2; medium (M), 0.062 m^2; large (L), 0.126 m^2; and extralarge (XL), 0.263 m^2). One half of the trays contained 4 plastic Bio-Spheres (ca. 5 cm in diameter) per compartment, which were included in an effort to increase surface area for fouling organisms. *A priori* contrasts use an adjusted decision rule (α') of 0.0127. *P* values in bold type indicate statistical significance.

Growth

Growth of lobster juveniles in flow-through bottles and dishes was unremarkable, and similar to that observed by Beal (2012); however, size of container played an important role in most field experiments (Tables 5, 6, 8, 10, and 11B; Figs. 6, 7, 9, and 10). Animals generally responded to an increase in container size with significant increases in mean CL or wet mass similar to that observed by Van Olst and Carlberg (1978) and Aiken and Waddy (1978) in the laboratory with cultured juveniles of *H. americanus*. For example, lobsters were ca. 33% larger and 140% heavier in Petri dishes than in the smaller volume bottles. In lantern nets, lobsters in buckets were 33% larger than lobsters in Petri dishes. The most dramatic example of the effect of container size on lobster growth occurred in the nursery trays. In the first experiment (floating trays), mean wet mass of lobsters in the largest compartments (0.26 m^2) was ca. 20% greater than those in the smaller compartments (Fig. 9). That experiment was conducted mainly during fall and winter, when seawater temperatures and metabolic rates were declining. The experiment using submerged trays, and conducted over

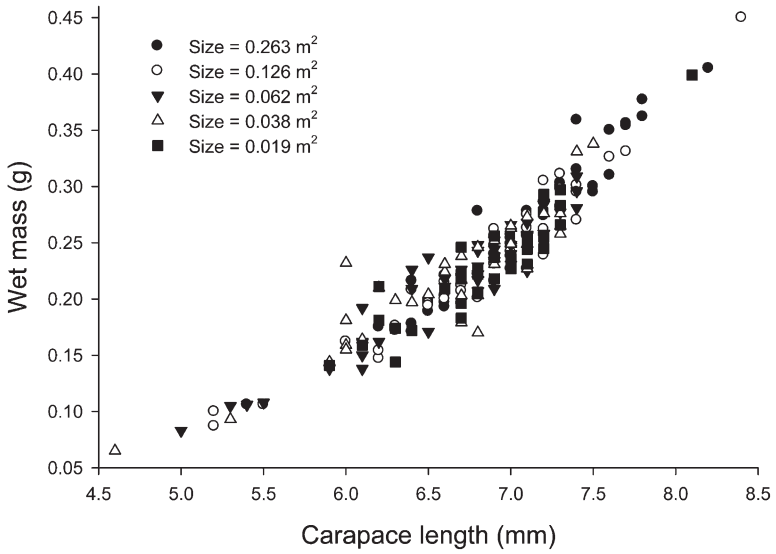

Figure 8. Effect of compartment size on the relationship between wet mass and carapace length (CL) of juvenile lobsters in nursery trays on January 3, 2005. Trays were deployed at Mud Hole Cove on September 2, 2004. Analysis of the ln-transformed regression lines indicated that the 5 lines were parallel ($P = 0.3352$) and that there was no overall effect on wet mass resulting from compartment size ($P = 0.0522$); however, ANOVA (Table 8) indicated that mean mass of lobster juveniles in the largest containers was significantly greater than the mean pooled mass of lobsters in the 4 smaller container sizes. ANCOVA revealed no statistically significant effect of biofouling balls on the relationship between wet mass and CL ($P = 0.7203$).

nearly 14 mo, demonstrated unambiguously that growth is a function of container size, as animals in the 2 largest compartments (0.13 m^2 and 0.26 m^2) attained a mean CL (23.9 ± 1.4 mm, $n = 23$) that was ca. 55% larger than the mean CL in the smallest compartment (0.019 m^2; 15.2 ± 0.9 mm, $n = 12$). These results help interpret why growth apparently was suppressed in bottles and Petri dishes in this and previous field trials (Beal 2012). In addition, a similar relationship may exist between container size and growth of European lobsters, *H. gammarus*. Knudsen and Tveite (1999) held cultured stage IV *H. gammarus* individually in flow-through containers (0.012 m^2 and 0.024 m^2) on soft bottoms (1.5–10 m) for 3 mo near His, Norway. The mean CL of animals in the larger containers was 10% larger than that in the smaller containers. Beal et al. (2002) used off-bottom nursery cages similar to those described in the current study to house flow-through containers (200 mL and 440 mL) holding individual *H. gammarus* for 10 mo off the Irish west coast. Final mean CL did not differ significantly between container sizes, but lobsters increased only ca. 50% in length. Benevente et al. (2010) held hatchery-reared *H. gammarus*

TABLE 8.

Analysis of variance on the mean mass of lobsters in floating trays in Mud Hole Cove, Beals, ME, on January 3, 2005.

Source of Variation	*df*	SS	MS	F	Pr > F
Bio-Spheres (present vs. absent)	1	0.0000	0.000	0.00	0.9765
Compartment	4	0.0555	0.0139	2.70	0.0501
XL vs. L, M, S, XS	1	0.0513	0.0513	9.99	**0.0037**
L vs. M, S, XS	1	0.0032	0.0032	0.63	0.4351
M vs. S, XS	1	0.0005	0.0005	0.10	0.7503
S vs. XS	1	0.0000	0.0000	0.01	0.9338
Cylinders × compartments	4	0.0362	0.0091	1.76	0.1634
Tray (cylinders)	29	0.1490	0.0051	1.64	**0.0275**
Error	177	0.5537	0.0031		
Total	215	0.7944			

Stage IV lobsters were placed into trays on September 2, 2004. Each of 32 trays contained 2 replicates of 5 compartment sizes (extrasmall (XS), 0.019 m^2; small (S), 0.038 m^2; medium (M), 0.062 m^2; large (L), 0.126 m^2; and extralarge (XL), 0.263 m^2). One half of the trays contained 4 plastic Bio-Spheres (ca. 5 cm in diameter) per compartment, which were included in an effort to increase surface area for fouling organisms. *A priori* contrasts use an adjusted decision rule (α') of 0.0127. *P* values in bold type indicate statistical significance.

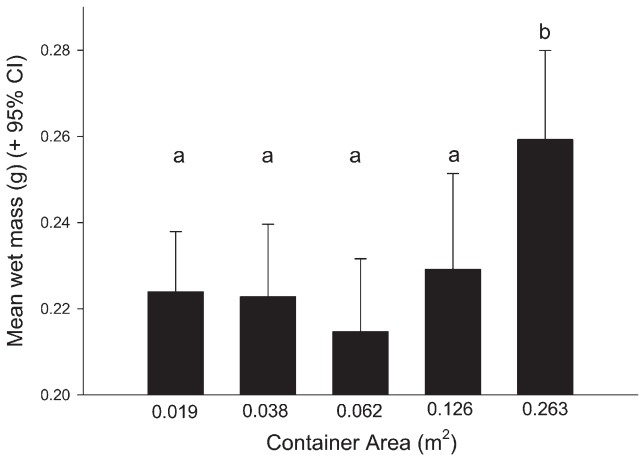

Figure 9. Mean wet mass of juvenile lobsters on January 3, 2005, that had been growing in wooden floating trays lined with window screening that were deployed on September 2, 2004, at Mud Hole Cove, Beals, ME. Lobsters were reared in various-size compartments in each tray (see Methods). Means with similar letters are not significantly different ($P > 0.05$). *n* varies from 47–51 lobsters.

TABLE 9.

Analysis of variance on the mean percent survival of cultured lobsters held in each of 3 sizes of flow-through containers (Petri dishes, 15 × 1 cm; squat plastic buckets, 20 cm in diameter × 15 cm in height; tall plastic buckets, 17 cm in diameter × 20 cm in height).

Source of Variation	*df*	SS	MS	F	Pr > F
Net	8	1.5185	0.1898	1.10	0.3662
Container	2	0.0648	0.0324	0.10	0.9802
Dish vs. bucket	1	0.0231	0.0231	0.07	0.7959
Buckets: tall vs. squat	1	0.0417	0.0417	0.12	0.7287
Net × container	16	5.3519	0.3344	1.94	**0.0212**
Tier (container)	5	0.6296	0.1259	0.70	0.6272
Net × tier (container)	40	7.2037	0.1801	1.04	0.4132
Substrate (tier, container)	6	2.7500	0.4583	3.14	**0.0111**
Net × substrate (tier, container)	48	7.0000	0.1458	0.85	0.7453
Error	144	24.8333	0.1725		
Total	269	49.3519			

Containers were arrayed within 9 lantern nets from August 2, 2006, to November 19, 2007, at Mud Hole Cove. Nets are considered a random factor, whereas level, container, and substrate (crushed shell vs. no shell) are all fixed factors. *A priori* contrasts for container appear directly below this source of variation, and use an adjusted decision rule (α') = 0.0253. *P* values in bold type are statistically significant.

postlarvae individually in suspended flow-through containers (1,520 mL vs. 643 mL) in Galicia, Spain, and found that specific growth rates of were 32% faster in the larger containers.

Collectively, results presented here and those from Europe suggest that the *in situ* scope for growth of early benthic phase wild juveniles of both *H. americanus* and *H. gammarus* during the first year may be greater than what has been observed (e.g., James-Pirri & Cobb 1997, Sheehy et al. 1999, Gendron & Sainte-Marie 2006). Wahle and Fogarty (2006) examined

TABLE 10.

Analysis of variance on mean carapace length of live cultured lobsters held in lantern nets at Mud Hole Cove, Beals, ME, from August 2, 2006, to November 19 2007.

Source of Variation	*df*	SS	MS	F	Pr > F
Net	8	34.09	4.26	2.70	0.0644
Container	2	83.66	41.83	12.07	**0.0011**
Dish vs. bucket	1	83.10	83.10	18.11	**<0.0001**
Buckets: tall vs. squat	1	0.56	0.56	0.12	0.6578
Net × container	13	46.35	3.57	2.26	0.0915
Tier (container)	5	15.51	3.10	0.89	0.5097
Net × tier (container)	16	51.29	3.21	2.03	0.1179
Substrate (tier, container)	5	5.98	1.19	0.39	0.8363
Net × substrate (tier, container)	4	12.34	3.08	1.96	0.1709
Error	11	17.33	1.58		
Total	64	266.55			

Lobsters were placed in 1 of 3 containers (Petri dish, squat bucket, or tall bucket; see Table 9 and Methods for specific sizes). Each lantern net had 10 tiers, but only the top 8 were used. *A priori* contrasts for container appear directly below this source of variation, and use an adjusted decision rule (α') = 0.0253. *P* values in bold type are statistically significant.

TABLE 11.

Analysis of variance on the untransformed mean number surviving (A) and mean carapace length (B) of juvenile lobsters held in submerged wooden trays (1.11 m^2) from August 12, 2009, to October 5, 2010 (419 days), at Mud Hole Cove, Beals, ME.

(A)

Source of Variation	*df*	SS	MS	F	Pr > F
Mesh (1.8 mm vs. 2 mm)	1	1.38	1.38	7.38	**0.0264**
Compartment size	4	0.17	0.04	0.17	0.9526
XL and L vs. M, S, XS	1	0.02	0.02	0.08	0.7792
XL vs. L	1	0.06	0.06	0.23	0.6350
XS vs. S and M	1	0.03	0.03	0.12	0.7315
S vs. M	1	0.06	0.06	0.23	0.6350
Mesh × compartment size	4	0.77	0.19	0.75	0.5633
Tray (mesh)	8	1.50	0.19	0.82	0.5927
Tray × compartment (mesh)	30	7.68	0.26	1.12	0.3591
Error	48	11.00	0.23		
Total	95	22.34			

(B)

Source of Variation	*df*	SS	MS	F	Pr > F
Mesh (1.8 mm vs. 2 mm)	1	2.69	2.69	0.13	0.7281
Compartment size	4	725.62	181.41	38.27	**<0.0001**
XL and L vs. M, S, XS	1	479.45	479.45	101.15	**<0.0001**
XL vs. L	1	3.16	3.16	0.67	0.4215
XS vs. S and M	1	43.03	43.03	9.08	**0.0062**
S vs. M	1	199.97	199.97	42.18	**<0.0001**
Mesh × compartment size	4	9.19	2.30	0.48	0.7468
Tray (mesh)	8	166.48	20.81	11.64	**<0.0001**
Tray × compartment (mesh)	23	109.02	4.74	2.65	**0.0173**
Error	19	33.96	1.79		
Total	59	1,046.96			

Ten of the 12 trays initially deployed were recovered. Five recovered trays were lined completely with fiberglass window screening (aperture, 1.8 mm), and the other 5 were lined with nylon screening (aperture, 2 mm). Each tray was subdivided into 5 compartments (extrasmall (XS), 0.019 m^2; small (S), 0.038 m^2; medium (M), 0.062 m^2; large (L), 0.126 m^2; and extralarge (XL), 0.263 m^2) that were replicated twice in each tray. Planned comparisons appear below the compartment size source of variation ($\alpha' = 0.0127$). *P* values in bold type are statistically significant.

length–frequency distributions of wild juveniles in Maine, and decomposed them into estimated age classes. They determined that mean CL (±SD) for the 2+ y class was 19.7 ± 3.7 mm, and that animals in the next year class averaged 24.1 ± 5.0 mm. Wild juveniles of *H. americanus* undergo a shift in behavior at CLs between 15 mm and 25 mm (Hudon 1987, Lawton & Lavalli 1995) when they begin to forage outside of their shelter. Until that time, growth may be limited by shelter-restricted behaviors (sensu Cobb 1971, Boudreau et al. 1990). In the largest predator-free compartments in submerged trays, lobsters in the current study attained CLs in ca. 14 mo (Fig. 10) that were similar to wild juveniles over 24+ mo in midcoast Maine (Cowan et al. 2001).

These results demonstrate that it is possible to rear cultured lobsters of approximately 4 mm in CL to sizes exceeding 20 mm in CL (an increase of nearly 400%) in flow-through containers as small as 0.13 m^2 (ca. 10 L) in ca. 14 mo in the cold waters off

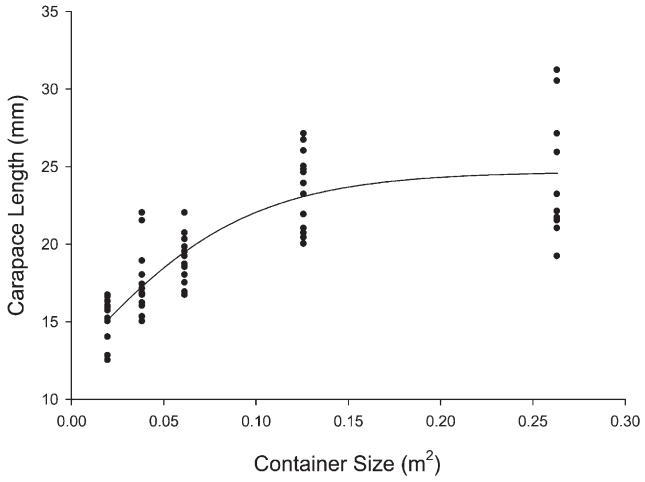

Figure 10. Relationship between carapace length (CL) and container size for cultured lobsters on October 5, 2010, that had been growing for 419 days in submerged wooden trays deployed on August 12, 2009, at Mud Hole Cove, Beals, ME. Approximately 68% of the variability in CL could be explained by container size using a sigmoidal function ($y = a/(1 + \exp(-(x - x_0)/b))$, where $a = 24.67$, $b = 0.048$, and $x_0 = -0.0024$ ($n = 61$, $r^2 = 0.6768$).

eastern Maine. Although the equipment and experimental design were intended to provide information to assess only the development, not commercial, phase of this effort, it is tempting to think about the implications of these results for stock enhancement. The nature of enhancement programs with American lobster postlarvae has been to release stage IV individuals that are not easily marked, highly susceptible to predation, extremely mobile, and may be developmentally delayed as a result of the rearing methods in the hatchery (Castro & Cobb 2005). The animals reared in the 2 largest

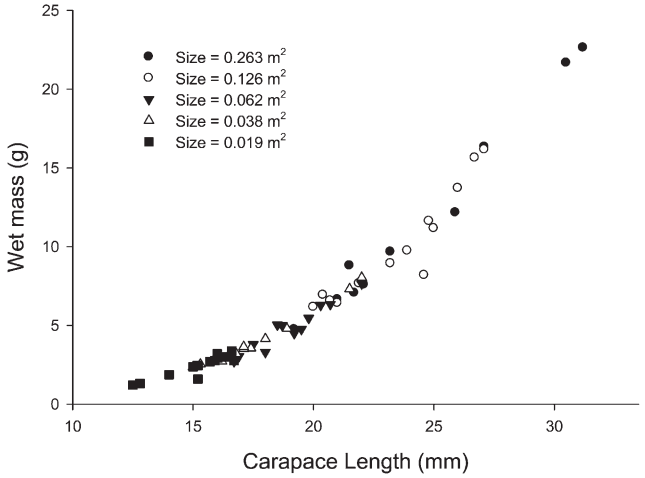

Figure 11. Relationship between wet mass and carapace length (CL) for cultured lobsters as described in Figure 10. Regression analysis showed that each of the ln-transformed lines associated with a particular compartment size had similar slopes ($P = 0.7331$), and ANCOVA demonstrated no effect resulting from compartment size on the mass–CL relationship ($P = 0.8160$). A power exponential function ($Y = aX^b$) resulted in the following equation: $Y = (3.448 \times 10^{-4})X^{3.239}$ ($r^2 = 0.980$, $n = 60$).

compartments of the submerged nursery trays would be considered vagile juveniles (sensu Lawton & Lavalli 1995), large enough to receive a physical tag (mean TL, 99.9 ± 6.8 mm; $n = 23$) that would not be lost immediately through molting, and could be seen easily by fishers or scientists on recapture (i.e., elastomer or streamer tagging systems; see Uglem et al. (1996) and Linnane and Mercer (1998)). In addition, vagile lobsters presumably would be less susceptible to predators than stage IV or stage V individuals (Wahle 1992, Spanier et al. 1998), and would have developed a relatively large, strong, functional crusher claw (Costello & Lang 1979, Govind & Pearce 1992). The relatively fast growth rates observed in the submerged trays should provide direction for finding cost-effective alternatives to enable hatcheries to produce large numbers of stage IV individuals (e.g., Browne & Mercer 1998, Beal & Chapman 2001), and to release large numbers of older animals (Tlusty et al. 2005). Future efforts should concentrate on finding or manufacturing an inexpensive container that will allow an adequate flow of seawater to eliminate the potential for high sedimentation rates and be large enough (ca. 0.13 m^2, 10 L) to maximize lobster growth. However, additional experimental work is required because it is unknown whether containers should be rectangular and narrow, round and tall, cuboidal, or some other configuration.

Although lobster growth was restricted by container size, animals surviving in field cages and trays for periods ranging from ca. 150–450 days fed by consuming organisms and/or detritus that drifted, settled into, and grew within the container housing them. The exoskeleton of all surviving animals appeared normally pigmented, and none were lethargic, suggesting that the available diet was at least adequate for maintenance. Sainte-Marie and Chabot (2002) were the first to examine the natural diet of juvenile (benthic) American lobsters (CL, 4–22.5 mm). At a site in the Magdalen Islands, Gulf of St. Lawrence, they found that bivalves and flesh (soft parts) were among the most common items in the diets of lobsters ≤20 mm in CL, occurring in 90% of stomachs examined. In addition, macroalgae occurred in 70% of stomachs of small lobsters. Ontogenetic shifts in diet occurred with increasing lobster size, as the smaller animals fed on more easily acquired food (including meiobenthic crustaceans and foraminiferans), whereas larger lobsters tended to feed on more mobile prey items. They did not find evidence of suspension feeding, as no planktonic organisms were identified from the stomachs of animals less than 20 mm in CL; however, Lavalli and Barshaw (1989) showed that recently settled postlarvae of *H. americanus* living in burrows may suspension feed. In the current study, it appears that lobsters had many dietary choices based on observations of organisms in the containers and compartments, ranging from bivalves (e.g., *Anomia simplex* D'Orbigny, 1842; *M. edulis; Hiatella arctica* (Linnaeus, 1767)) to crustaceans (*Semibalanus balanoides* (Linnaeus, 1767)), and polychaetes (e.g., *Amphitrite cirrata* (O. F. Müller, 1771), *Alitta virens* (M. Sars, 1835), *Nephthys caeca* (Fabricius, 1780), *Nephthys ciliata* (Müller, 1776)). In addition, other species such as the tunicate *Ciona intestinalis* (Linnaeus, 1767) and the encrusting sponge *Cliona celata* Grant, 1826, were commonly found both on the outside and inside of containers and compartments, but they were most often large (>50 mm), and appeared not to have been consumed when they occurred together with the live lobsters.

Communal Rearing

Communal rearing of the early juvenile lobster stages (Aiken & Waddy 1988) compared with other grow-out systems may be an attractive alternative to field-based lobster nurseries given the low costs associated with materials, deployment, and maintenance. Our attempts to rear animals communally during a 51-day period during fall 2005 in piles of mussel shells inside a tank receiving ambient, flow-through seawater at DEI resulted in poor survival (<10%). Shells were not prefouled, so animals would have had access only to detritus and microscopic settlers from the plankton, as they did in the submerged nursery cages. This may have been a food-limited system, which could explain the high mortality over such a relatively short time. In addition, the habitat configuration that the shells provided may not have been adequate for the size of lobster used (Aiken & Waddy 1995). Several attempts at communal rearing of wild and cultured *H. americanus* postlarvae in the laboratory or field have yielded results similar to those observed in the current study (e.g., Van Olst et al. 1975, Sastry & Zeitlin-Hale 1977, Carlberg et al. 1979, Johns & Mann 1987, Castro et al. 2001). The success of communal rearing with cultured individuals of *H. gammarus* has been more variable, with short-term survival rates ranging from 5–67% (Linnane et al. 2000, Jørstad et al. 2001, Beal et al. 2002). Most studies supplemented natural diets with *Artemia* or mysid shrimp. Recently, Uglem et al. (2006) compared survival of stage IV *H. gammarus* held in communal, land-based tanks with those in sea-based culture in individual cages over a 210-day period in Galicia, Spain. In addition to natural, epibiotic organisms that fouled the mussel shells (*M. edulis* and *Mytilus galloprovincialis* Lamarck, 1819), the diet of animals in the communal rearing system was enhanced with shrimp dry pellets. Communal survival was 28% compared with 89% in the sea cages, and growth was more variable in the communal system (Uglem et al. 2006). Collectively, results from trials using both species of homarid lobsters suggest that communal rearing is not a viable alternative to produce large quantities of lobsters for stock enhancement activities.

Other Potential Uses for Cultured H. americanus *Juveniles*

Beal (2012) suggested 2 additional uses for cultured lobster juveniles besides public stock enhancement programs or for sale for research purposes (M. Tlusty, New England Aquarium, Boston, MA, pers. comm.). These include the aquarium trade and human consumption. American lobsters have never been sold for the aquarium trade presumably because state and federal regulations and laws protecting the commercial fishery prohibit the possession of sublegal animals. In Maine, for example, fishers can have their lobster fishing license suspended for up to 3 y based on 2 or more convictions of possessing short (CL, <82.6 mm) lobsters (§6402-B, Chapter 617, State of Maine Marine Resources Lawbook; http://www.maine.gov/dmr/lawsandregs/lawbook9-12-09.pdf). Because landings of lobsters in the northeast United States is geographically variable, and it is possible to rear large numbers of larvae year-round (Aiken & Waddy 1985), the potential exists to diversify economically the lobster industry by producing stage IV or larger juveniles for the aquarium trade. Cultured American lobster juveniles can be reared at room temperature (ca. 20–25°C) in various-size aquaria for more than 2 y (B. Beal, pers. obs.), and provide excellent educational opportunities for classroom projects (D. Carver, 7th grade science/mathematics teacher, Jonesport Elementary School, Jonesport, ME, pers. comm.). In addition, care and handling guidelines for tropical lobsters (e.g., *Enoplometopsus* spp.) and other ornamental decapods (Calado et al. 2007) are appropriate for aquarium culture of American lobsters (B. Beal, pers. obs.). In addition, it is possible to rear cobalt blue lobsters from blue parents (Beal et al. 1998) that would likely be more valuable than the phenotypic brownish green color of wild animals.

The mean wet weight of lobsters in the 2 largest compartments of the submerged tray experiment (experiment V) was 10.7 ± 8.6 g ($n = 23$, maximum = 22.6 g), which is similar in size to the crawfish *Procambarus clarkii* (Girard, 1852) and *Procambarus zonangulus* Hobbs, Jr. and Hobbs III, 1990, that are cultured commercially in the southeast United States (Mazlum & Eversole 2005) and sold domestically (Romaire et al. 2005). If federal and state laws and regulations were to permit the sale of sublegal, hatchery-reared animals, it may be possible to market and sell 1- or 2-y-old cultured *H. americanus* juveniles domestically or internationally using the low-cost grow-out methods described here. New, cultured products for human consumption would create jobs in the lobster industry, and would help stabilize economies in coastal communities where production of wild lobsters has declined precipitously in recent years (Stevens 2009, Wahle et al. 2009).

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