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METHODS FOR MASS REARING STAGES I–IV LARVAE OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS* H. MILNE EDWARDS, 1837, IN STATIC SYSTEMS

BRIAN F. BEAL[1,*] AND SAMUEL R. CHAPMAN[2]

[1]*University of Maine at Machias, 9 O'Brien Avenue, Machias, Maine 04654;* [2]*Waldoboro Shad Hatchery, Waldoboro, Maine 04572*

ABSTRACT We conducted a series of five laboratory experiments (7–18 days in duration) to test the interactive effects of stocking density, aeration rates, and food types on survival of American lobster (*Homarus americanus*) larvae through their first three planktonic stages (I–III) to the postlarval stage (IV). Experimental units and culture protocols were designed to replicate a 1:100 scaled-down version of equipment used in association with a fishermen-sponsored, stock enhancement lobster hatchery located in Cutler, Maine. The first four trials revealed that extremely high rates of aeration (ca. 240 mL air sec^{-1}) were necessary to distribute larvae and food sufficiently to reduce cannibalistic encounters; however, the best survival from stage I–IV (at stocking densities of 7–26 L^{-1} fed *ad libitum* with enriched *Artemia*) was only 24%. The final experiment (stocking density = 20 L^{-1}) yielded a mean survival rate (± 95% CI) of 75.8 ± 10.2% (range = 62.7% to 90.7%; n = 6). One important difference between the last and first four experiments was how stage I larvae were managed prior to their culture. In the first four trials, unfed larvae were collected from a relatively small (46 cm × 30 cm × 20 cm), screened capture basket located near the discharge pipe of a broodstock holding tank at the hatchery where they may have resided for > 12 hr. Larvae used in the final laboratory experiment were collected directly from the broodstock tank within 30 min after being liberated from the mother's swimmerets. Larvae, at relatively high densities within the screened box, likely had many more cannibalistic encounters prior to their culture than those collected directly from the broodstock tank and, therefore, suffered high rates of mortality during the first four laboratory trials. Mass rearing methods for larval American lobsters developed in conjunction with these laboratory experiments were used successfully by staff at the Cutler Marine Hatchery from 1988 to 1992. During this period, survival from stages I–IV averaged 44%, and approximately 875,000 stage IV animals were released to the wild. These culture methods have withstood the test of time as a private lobster hatchery in Maine adopted our protocols in 1993, and they continue to be in use. Further, the general techniques described here have been used since 1994 to culture European lobsters (*Homarus gammarus*) at a commercial lobster hatchery in the southeast of Ireland.

KEY WORDS: lobster, *Homarus americanus*, culture, static systems, stock enhancement, *Artemia*, microalgae, stage IV larvae

INTRODUCTION

Mass production of juvenile lobsters (*Homarus americanus* H. Milne Edwards) for stock enhancement programs began as early as 1872 in the United States (Rathbun 1886). Lobster "parks," natural tidal impoundments, were used in Maine and Massachusetts as spawner sanctuaries where egg-bearing females were held until releasing their stage I larvae. The earliest lobster hatchery was established in 1883 at Woods Hole, Massachusetts. Here, eggs were detached from females, placed into hatching jars, and stage I lobsters released to the wild (Nicosia and Lavalli 1999). In time, enhancement of lobster stocks using early planktonic individuals was abandoned in favor of methods to rear larvae for release at their earliest benthic stage (reviewed in Nicosia & Lavalli 1999).

Perhaps the most successful long-term stock enhancement effort in the United States with respect to juvenile production occurred at the Massachusetts State Lobster Hatchery and Research Station on Martha's Vineyard from 1951 to 1997. Culture protocols and equipment were developed that became the standard for production of massive numbers of stage IV individuals (Hughes 1972, Hughes et al. 1974). In particular, a 40-L round-bottom rearing vessel, or kreisel, was invented that, with sufficient flow rates (ca. 10 L min^{-1}), provided enough turbulence to distribute homogeneously both larvae and food, and minimized cannibalistic encounters (Hughes et al. 1974). Stocking these kreisels with 2,000 stage I larvae of *H. americanus* and supplying them with live brine shrimp (*Artemia salina* L.) during the ten to fourteen days in culture reportedly resulted in survival rates to stage IV between 75%–85% (Hughes et al. 1974, Serfling et al. 1974a, Schuur et al. 1976, Van Olst et al. 1980, Aiken & Waddy 1989, Waddy and Aiken 1998). Improvements on the basic design enabled the culture system to operate efficiently either using recirculating or flow-through seawater (Serfling et al. 1974a, Schuur et al. 1976, Van Olst et al. 1977). During the past three decades, the "Hughes pot," or planktokreisel, has been used widely by scientists in the United States and Canada to produce large numbers of juvenile lobsters for enhancement of wild stocks, commercial operations, and laboratory and field experiments. In addition, similar larval culture systems have been used in Europe with *H. gammarus* L. (Beard & Wickins 1992, Burton 1992, Browne 1999).

In Maine, during the mid-1980's, lobster fishers decided they wanted to fund up to five lobster hatcheries along the coast to produce stage IV individuals for stock enhancement purposes (Plante 1986). At the same time, one of us (S. Chapman) was working on a simple system to rear lobster larvae from stages I–IV in 400-L conical tanks similar to those used to culture bivalve larvae (Castagna 1983). The process involved culturing phytoplankton to enrich brine shrimp that were then added (after a period of growth) to static culture tanks containing lobster larvae. The work was carried out primarily because Chapman was unable to repeat the success of others using the smaller 40-L kreisels (Hughes et al. 1974) and he was interested in developing culture protocols that could be transferred easily to groups of fishers.

In 1986, the first fishermen-sponsored stock enhancement program for lobsters in Maine was initiated in the eastern coastal community of Cutler, and the Cutler Marine Hatchery (CMH) was created (Nicosia & Lavalli, 1999). From 1986 to 1992, this program was the only enhancement effort funded by lobster license fees through Maine's Department of Marine Resources. Although we both served as technical advisors to CMH during this time, the

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

hatchery was managed by a fisherman and elderly housewife who, before that time, had no technical training in any aspect of the biological sciences.

During the first months of production at CMH in 1986, survival rates of stage I–IV lobster were very poor (< 10%). Here, we describe a series of five sequential laboratory experiments conducted between July and October 1986 that were designed to improve on this survival rate.

MATERIALS AND METHODS

A series of five larval lobster culture experiments (A–E) were conducted at ambient room temperatures at the University of Maine at Machias (UMM) between 15 July and 17 October 1986. Experiments were designed to assist staff at the CMH with culture protocols to maximize lobster larvae survival from stages I to IV. At UMM, it was not possible to replicate the culture vessels employed at Cutler's Hatchery (ca. 400-L conical-shaped fiberglass tanks filled to 375 L and aerated from the apex of the cone). Instead, we used 4.73-L plastic, flat-bottomed, round buckets (25.4 cm diameter at the top, tapering to 20.3 cm diameter at the base). A 3.2 mm hole was drilled in the middle of the bottom of each bucket (experimental unit) and a ceramic air stone fitted into each hole. A piece of tubing connected each ceramic stone to a manifold that received a supply of air from a pump (1-hp Conde, Westmoor Ltd., Sherill, NY). All experiments were conducted in 3.78 L (1 gallon) of seawater, which represented approximately 1/100th of the water volume used at Cutler. Buckets were not covered; therefore, photoperiod varied from one experiment to another. An attempt was made to determine if experimental results could be repeated at the Cutler Marine Hatchery (see Results—Experiment B).

Stage I lobster larvae used in Experiments A–D (Table 1) were collected at 0700 hr from a screened wooden box (46 cm × 30 cm × 20 cm) located near the discharge pipe of a broodstock holding tank at CMH, where they may have resided for > 12 hr. Larvae were transferred immediately to moist paper toweling nested within a stainless steel sieve (64 μ), placed inside a styrofoam cooler, and transported to UMM (a process that took between 30 to 45 min). Larvae used in Experiment E were taken directly from the broodstock tank with a small fish net only moments after they had been liberated from the mother's swimmerets (*sensu* Talbot and Helluy, 1995). Filtered (1 μ) seawater used in all experiments was collected at CMH.

At UMM, larvae were immediately transferred to a 40-L aquarium from which individuals were removed, counted, and added to experimental units containing a source of food (see below). We assumed that animals transferred to experimental units were unaffected by our handling, although we did not conduct a specific handling experiment. We used only larvae that were swimming prior to initiating each experiment. Every 48 hours until the end of an experiment, larvae in this static culture system were poured through a nylon fish net (1 mm aperture) that retained

TABLE 1.

Duration and treatments used in Experiments A (n = 4), B–D (n = 3), and E (n = 6).

Experiment	Duration[1]	Density/unit[2]	Food type[3]	Aeration rate[4]
A	15–21 July	100	LBS	Low
		100	LBS	Moderate
		150	LBS	Low
		150	LBS	Moderate
B	28 July–11 August	100	LBS	Moderate
		100	LBS	High
		150	LBS	Moderate
		150	LBS	High
		200	LBS	Moderate
		200	LBS	High
C	11–25 August	50	Clam	High
		50	FBS	High
		100	Clam	High
		100	FBS	High
		150	Clam	High
		150	FBS	High
D	4–22 September	25	Clam + LBS	High
		25	Mackerel + LBS	High
		50	Clam + LBS	High
		50	Mackerel + LBS	High
		100	Clam + LBS	High
		100	Mackerel + LBS	High
E	1–17 October	75[a]	LBS	High
		75[b]	LBS	High

[1] Experiments conducted in 1986.
[2] Number per 3.78 L (1 gallon).
[3] LBS = Live, enriched Brine Shrimp; FBS = Frozen Adult Brine Shrimp.
[4] Low = 20 mL air sec^{-1}; Moderate = 80 mL air sec^{-1}; High = 240 mL air sec^{-1}.
[a] Octagonal strips (33 cm × 33 cm) of black plastic mesh (6.4 mm aperture) added to each experimental unit
[b] Control: no plastic strips added to experimental units

larvae and any uneaten food. Larvae were returned immediately to a clean (rinsed with 60°C freshwater) bucket containing 3.78 L of seawater (room temperature) and food.

Live brine shrimp (*Artemia salina*), used as a source of food in Experiments A, B, D, and E, were reared in 40-L glass aquaria at UMM. *Artemia* were fed algae (Tahitian *Isochrysis galbana* Parke [clone T. iso] and *Chaetoceros gracilis* Ehrenberg) *ad libitum* that had been cultured at CMH. Brine shrimp were cultured for four days (total length ca. 2–3 mm) at a temperature of 30°C under constant fluorescent lighting before transferring to experimental units (ca. 40 brine shrimp per mL). In all experiments, there was always an excess number of live brine shrimp in experimental units after 48 hours. This number was estimated by counting a 1 mL sample from each unit using a Sedgewick-Rafter cell. These excess brine shrimp were returned to the experimental unit from which they had come and new, four day-old brine shrimp were added to bring the density to 40 mL^{-1}.

In Experiments A and B (Table 1), aeration rate was one of two factors tested. Altogether, three aeration rates were examined (Low = 20 mL air sec^{-1}, Moderate = 80 mL air sec^{-1}, High = 240 mL air sec^{-1} as measured crudely using a water displacement technique). Qualitatively, the low flow rate resulted in a few small air bubbles per second. Water movement was minimal and restricted to a small column the width of the air stone (ca. 20 mm) in the center of each bucket. At low aeration, both larvae and brine shrimp were visible; however, lobster larvae appeared to congregate on or near the bottom of the buckets. With moderate aeration rates, water motion also was restricted to the center of the buckets, although the diameter of the circulation zone was larger (ca. 80 mm). At this flow rate, larvae were moved in a gentle upward motion and then immediately downward in a vertical circulating current. High rates of aeration resulted in vigorous vertical and lateral movement of larvae throughout the water column. Larval motion was too rapid to observe individuals. At these aeration rates, the water surface within each bucket was moving so rapidly that it appeared to be boiling.

Experiments A–D were completely factorial with two fixed factors per trial. Experiments were sequential in that results from a particular trial were used to design the ensuing trial. In Experiments C and D, food type was varied. For Experiment C, 6–8 mm pieces of fresh soft-shell clam, *Mya arenaria* L., mantles and similar sized frozen adult brine shrimp were used to feed lobster larvae. In Experiment D, 6–8 mm pieces of fresh clam and frozen and thawed muscle tissue from mackerel (*Scomber scombrus* L.) were added to experimental units containing live, algal-enriched brine shrimp. In Experiment E, octagonal strips (33 cm × 33 cm) composed of extruded, black plastic netting (6.4 mm aperture) were positioned at a 45° angle within six experimental units. Netting extended from the bottom of the experimental unit to a few cm above the surface of the seawater. The purpose of the netting was to increase spatial heterogeneity within the experimental units and provide a surface or substrate for larvae to encounter and, potentially, reduce conspecific cannibalistic encounters. Another six units served as controls (no netting).

For Experiments A–D, a two-factor, model I analysis of variance (ANOVA) was performed on the angular-transformed percent survival data (Sokal and Rohlf 1995). Orthogonal, *a priori* contrasts were performed for each source of variation with more than a single degree-of-freedom (see Results). A single-factor, model I ANOVA was performed on the angular-transformed percent survival data from Experiment E. In all cases, the transformation served to either normalize the data (Shapiro-Wilks test [SAS 1998]) and/or homogenize variances (Cochran's Test [Winer et al. 1991]).

RESULTS

Experiment A

The experiment was terminated on day seven because excessive heat inside the laboratory on 21 July (32°C), in addition to high cannibalism rates during the first six days, resulted in the deaths of 98% of the larvae. Only 41 stage III individuals of the initial 500 larvae stocked in the experimental units (Table 1) were alive on 21 July. There was no cumulative effect on survival to this stage due to density ($P = 0.094$); however, nearly 9× as many larvae survived the seven-day trial in experimental units receiving moderate (37 animals) versus low (4 animals) rates of aeration ($P = 0.021$).

Experiment B

Seawater temperature varied throughout the experiment from 19° to 24°C, which is within the range of natural conditions experienced by *H. americanus* larvae (Van Olst et al. 1980). Salinity was constant at 31 ppt. Eight days after the experiment was initiated, a mean of at least 88% mortality had occurred in all treatments (Table 2). By this date, all surviving larvae ($n = 216$) had reached stage III in their development. On 11 August, fourteen days after the experiment was initiated, only 124 of 900 (13.8%) larvae remained across all six treatments of which 119 (96%) had metamorphosed to stage IV. ANOVA revealed that all main and interaction sources of variation were significant ($P < 0.05$; Table 3). The effect of aeration rate on mean survival depended on stocking density. *A priori* contrasts indicated that 7.7% of the larvae reared at 100 $unit^{-1}$ (ca. 26 L^{-1}) survived from stage I to IV independent of aeration rate. This was nearly twice the average

TABLE 2.

Percent survival (±95% CI) of larval lobsters in Experiment B (28 July to 11 August 1986).

Density	Aeration	Day 6	Day 8	Day 10	Day 12	Day 14
100	Moderate	21.5 (12.35)	9.7 (1.47)	7.3 (1.43)	6.0 (4.31)	5.7 (2.87)
	High	18.0 (9.43)	12.7 (6.25)	11.3 (6.22)	10.7 (6.25)	9.7 (6.25)
150	Moderate	13.3 (8.72)	5.6 (6.69)	4.9 (6.27)	2.7 (4.38)	1.9 (1.65)
	High	18.6 (6.65)	10.4 (3.40)	7.8 (7.47)	9.2 (8.29)	6.9 (4.17)
200	Moderate	15.5 (6.95)	5.5 (5.46)	4.7 (2.58)	3.9 (4.30)	3.2 (2.46)
	High	9.8 (7.56)	7.3 (10.03)	4.8 (4.70)	4.5 (1.25)	3.2 (3.99)

Density = number per 3.785 L. Aeration (Moderate = 80 mL air sec^{-1}; High = 240 mL air sec^{-1}). Day refers to days after hatching. $n = 3$.

TABLE 3.

ANOVA on the angular-transformed survival data from Experiment B (11 August).

Source of variation	df	Sum of squares	Mean square	F value	Pr > F
Aeration	1	66.59	66.59	17.43	0.0013
Density	2	106.76	53.38	13.98	0.0007
(100 vs. [150 & 200]/2)	1	100.28	100.28	26.26	0.0003
(150 vs. 200)	1	6.48	6.48	1.70	0.2172
Density × Aeration	2	36.47	18.23	4.77	0.0298
(100 vs. [150 & 200]/2) × moderate vs. high	1	0.44	0.44	0.11	0.7412
(150 vs. 200 × moderate vs. high)	1	36.03	36.03	9.44	0.0097
Error	12	45.83	3.82	—	—
Total	17	255.65	—	—	—

A priori contrasts appear with density and interaction sources of variation. See Table 2 for aeration rates. $n = 3$.

survival rate (3.8%) of larvae at the two higher densities ($P = 0.0003$). High aeration rates significantly improved survival rates of larvae stocked at 150 unit^{-1} (40 L^{-1}) compared with moderate aeration rates, but this same improvement did not occur for larvae initially stocked at 200 unit^{-1} (53 L^{-1}).

Because this experiment had shown that high aeration rates (ca. 240 mL air sec^{-1}) and a density of 100 L^{-1} may result in 5–10% survival, a two-week test of these culture variables was initiated in three 400-L conical tanks at CMH from 11 to 25 August. Culture vessels at Cutler were treated similarly to those in the laboratory. We used algal-enriched, live brine shrimp (40 mL^{-1}) as a source of food and added approximately 10,000 stage I larvae to each vessel, which was aerated vigorously. A regression equation was developed using mass (g) and larval number to estimate number of stage I larvae stocked per conical tank (Fig. 1a) and number of stage IV larvae (Fig. 1b). These equations enabled us to estimate percent survival on a per-tank basis over the two-week culture period at CMH.

Culture conditions at Cutler were very similar to those at UMM. Seawater temperature varied between 20° and 24°C and salinity was 31 ppt during the two-week interval. Survival of stage I to IV larvae in the three conical tanks was: 7.5%, 10.2%, and 4.9%.

Experiment C

Previous experiments had demonstrated that mortality between stages I and III was severe (usually > 90%) in both the large conical tanks at CMH and the experimental units at UMM. Because we observed many cannibalistic encounters during the first week, one possible explanation for this might be that larvae preferred a larger food particle than the 2–3 mm brine shrimp.

Seawater temperature varied between 21.5° and 24°C and salinity fluctuated between 31 and 34 ppt. On 15 August, four days after the experiment was initiated, survivorship summed across all treatments was 24.1% (Table 4). When the experiment was terminated on 25 August, mean survivorship over all treatments was 1.5%. ANOVA (Table 5) demonstrated both a density and food type effect. Larvae survived best (2.4%) at the lowest density (50 unit^{-1}) and frozen brine shrimp provided a significantly higher survival rate (1.9%) than chopped soft-shell clam (1%) ($P = 0.0307$, Table 5).

Experiment D

Because the extremely poor survival rates observed in the previous experiment suggested that larger food particles, alone, should be rejected as a source of food for culturing lobster larvae, we examined the interactive effects of diet (large food particles [6–8 mm pieces of clam and mackerel] together with live brine shrimp) and stocking density (25, 50, 100 larvae unit^{-1}).

Seawater temperature varied between 17° and 23°C and salinity between 31 and 35 ppt during the 18-day trial. On 16 September, an experimental unit from the low-density fish treatment was found without water. All larvae inside were dead and this replicate was removed from the experiment. During the final two days of the experiment (20 to 22 September), all four larvae found in one experimental unit from the high-density fish treatment appeared to have become infected with the ciliate *Vorticella* spp. No other larvae appeared to have the ciliate.

Unlike previous experiments, overall mortality did not exceed 80% until the 16th day of the experiment (20 September, Table 6). The experiment was terminated on day eighteen when 96% of the individuals had metamorphosed to stage IV (Table 7). Because it is not possible to separate efficiently stage III from stage IV individuals, Table 7 can be used as a guide in developing strategies for releasing early benthic phase *H. americanus* from hatcheries (such as Cutler) that do not have space to rear stage IV + animals to larger sizes either individually or communally. For example, on Day 14, 35% of the animals were at stage III while 65% were at stage IV ($0.65 \times 180 = 117$ stage IV individuals). Two days later, 94% of the remaining larvae were stage IV ($.94 \times 143 = 134$). The additional 48 hours yielded 15% more stage IV individuals even though the percent of individuals reaching the fourth stage increased over this same time interval by nearly 30% (65% to 94%). This suggests that both overall percent survival and percent of individuals that have attained the first benthic stage should influence decisions when to release larvae to the wild.

ANOVA (Table 8) was unable to detect a difference in mean survival between the two food types (clam + live brine shrimp = 19% vs. mackerel + live brine shrimp = 13%, $P = 0.084$). There was no overall effect due to density; however, the *a priori* contrast of low (22%) vs. the mean of the two higher densities (13%) was significant ($P = 0.048$).

Although mean survival at the lowest density was better than in previous experiments (Table 6), these rates were much lower than published accounts of lobster larval survival to stage IV, either by other public hatcheries (e.g., the Massachusetts State Lobster Hatchery at Oak Bluffs, Martha's Vineyard, MA, Hughes et al., 1974) or research laboratories (Serfling et al. 1974; Schuur et al. 1976; Aiken et al. 1981; Eagles et al. 1984).

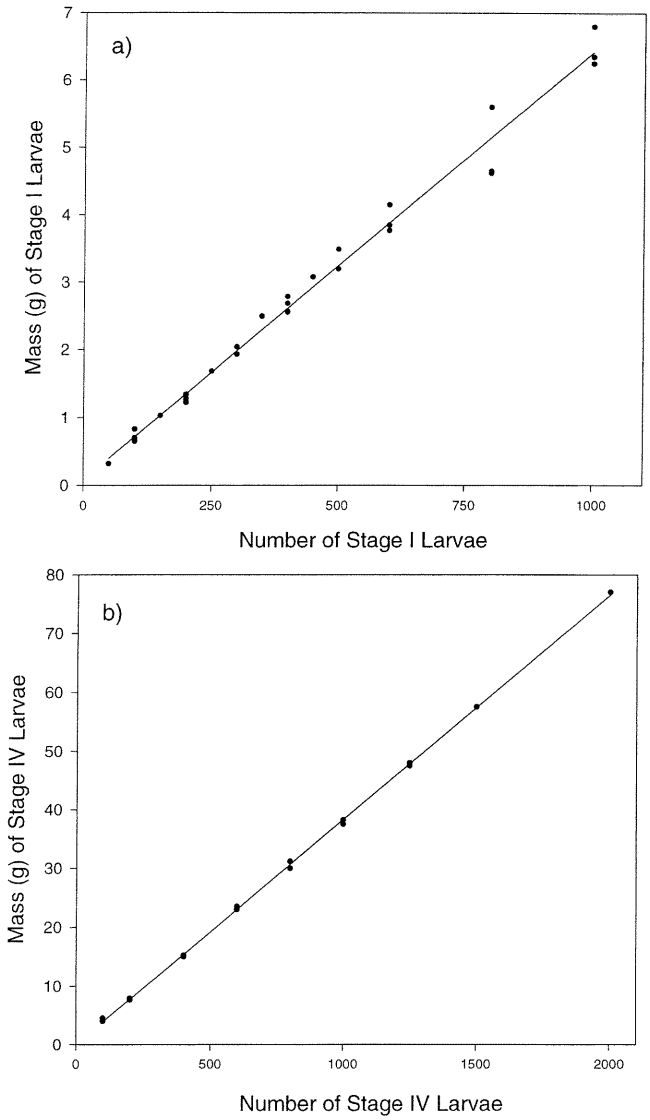

Figure 1. Mass(g)-to-number relationships for stage I (a) and IV (b) larvae of *Homarus americanus*. (Stage I: Y = 0.0824 + 0.00633 X, n = 30, r^2 = 0.988, 157.9 larvae g^{-1}; Stage IV: Y = 0.0896 + 0.03821 X, n = 16, r^2 = 0.999, 11.2 larvae g^{-1}). Larvae of both stages were caught using a nylon mesh (1 mm aperture) and transferred to a sieve (125 μ). A piece of paper toweling was used to absorb moisture from the bottom of the screening for 30 seconds before measuring mass using a Sartorius electronic balance to the nearest 0.01 g.

Experiment E

Seawater temperature varied between 17° and 22°C and salinity between 30 and 33 ppt. For no apparent reason, all larvae within one of the buckets containing a strip of the plastic netting died within the first 36 hours. On Day 15, 83% of all surviving individuals had reached stage IV. When the experiment was terminated 48 hours later, 98% had metamorphosed to stage IV. Dramatic differences in survivorship occurred between this test and all previous experiments (Fig. 2). By the end of the experiment, 18.1 ± 13.9% (95% CI) (range = 6.7% to 34.7%) of the animals in the experimental units containing plastic strips had survived to stage IV whereas 75.8 ± 10.2% (range = 62.7% to 90.7%) of the larvae attained stage IV successfully in the control units. These survival rates were highly significantly different ($P < 0.0001$)

Transfer of Techniques from the Laboratory to the Cutler Marine Hatchery

In 1986, an estimated total of 20,000 stage IV lobsters were released from CMH. The best survival rates observed during that season, which lasted from mid-June to mid-September was 12.5% (25 August to 9 September; Beal, pers. obs.). In 1987, using techniques learned from Experiment E (above), approximately 93,000 stage IV animals were released from CMH during a similar time interval. Survival rates were as high as 60%, but averaged 42% for the year (Beal, unpubl. data). From 1988 to 1992 (the last year CMH operated), an average of 175,000 stage IV lobsters per year were released by staff at CMH into coastal waters near Cutler, Maine (Beal et al. 1998). During that time, survival in the 400-L conical tanks varied between 25% and 65% with an average of 44%.

DISCUSSION

Experimental results and observations involving the initial handling of stage I lobster larvae described here led to the adoption of culture techniques that enabled staff at Cutler's Marine Hatchery to become successful in rearing *Homarus americanus* larvae through their planktonic stages (I–III) to first benthic stage (IV) for stock enhancement purposes. That program operated from 1986 through 1992 when public funding for lobster hatcheries in Maine ceased. The culture techniques described below have been in use since 1993 by staff at a private facility in Maine (the Southwest Harbor Oceanarium, SHO) who are engaged in stock enhancement efforts in the waters near Bar Harbor, Maine (T. Montague, hatchery manager, SHO, pers. com., 7 July 2000). In addition, similar culture techniques have been adopted for *Homarus gammarus* production of stage IV animals for stock enhancement efforts in Ireland (Browne & Mercer 1988).

In Maine, wild broodstock were obtained from fishers on an as-needed basis. Maine's Department of Marine Resources issued special permits annually to those who were active in the CMH stock enhancement program. (Aiken and Waddy [1985] reported that in Canada, it was difficult to obtain egg-bearing females from fishers. This led them to develop methods to domesticate broodstock for year-round seedstock production). In eastern Maine, broodstock with eggs ready to hatch (i.e., those that display a light bluish hue), were commonly available beginning the second week of June through mid-September from 1986 to 1992 (Beal, pers. obs.). Beginning in 1987 and continuing through the 1992 season, egg-bearing females entering CMH were immediately bathed in a 1% solution of Betadyne (povidone iodide) in filtered (1 μ) seawater to remove fauna and ectoparisites such as copepods, nematodes, or *Vorticella* spp., as well as reduce the probability of bacterial infections. The bath consisted of immersing the entire animal, except its mouthparts and gills, for 8–10 min. Egg-bearing females were then moved to a static, communal tank (1,320 liters) that was completely covered to provide constant darkness. No more than five female lobsters were held in this tank at any time. Ambient, filtered (1 μ) seawater in the tank was changed every two days and the tank thoroughly cleaned on a weekly basis. Hatching occurred generally throughout the day, but the hatching period for a particular female lasted no more than five days (see Hughes and Matthiessen 1962). Stage I swimming larvae were taken from the broodstock tank within 30 min of being expelled from the clutch using a small nylon aquarium fish net. Sometimes, large batches of stage I larvae were available early in the morning

TABLE 4.

Percent survival (±95% CI) of larval lobsters in Experiment C (11–25 August 1986).

Density	Diet	Day 4	Day 6	Day 8	Day 10	Day 12	Day 14
50	*M. arenaria*	30.0 (4.97)	13.3 (22.39)	5.3 (5.73)	2.0 (0.00)	2.0 (0.00)	2.0 (0.00
	Brine shrimp	30.0 (30.22)	16.7 (28.68)	8.0 (9.94)	4.7 (2.87)	3.3 (5.74)	2.7 (2.87)
100	*M. arenaria*	20.0 (7.45)	7.0 (9.93)	3.0 (4.97)	1.7 (3.79)	1.0 (2.48)	0.7 (1.43)
	Brine shrimp	30.7 (19.92)	13.3 (10.34)	8.3 (8.69)	4.3 (7.99)	2.0 (2.48)	2.0 (2.48)
150	*M. arenaria*	18.0 (7.22)	8.0 (3.32)	3.3 (2.87)	2.2 (3.45)	0.7 (1.66)	0.4 (0.96)
	Brine shrimp	15.6 (9.98)	6.4 (3.82)	2.9 (2.52)	2.2 (0.95)	1.3 (0.00)	0.9 (0.96)

Density = number per 3.78 L. Aeration (High = 240 mL air sec^{-1}). Diet (6–8 mm pieces): soft-shell clam (*M. arenaria*) or frozen brine shrimp. Day refers to days after hatching. $n = 3$.

(i.e., after CMH staff came to work ca. 0700); however, these larvae were not added to culture tanks. Instead, they were liberated because results from Experiments A–E suggested that a dense assemblage of unfed stage I larvae would not do well under culture conditions.

After collecting recently hatched larvae, each netted batch was weighed to provide an estimate of numbers placed into a 400-L culture tank (Fig. 1a). Over a two-day period, between 7,500 and 10,000 stage I larvae were added to a vigorously aerated (from the apex of the cone) conical tank filled to ca. 375 L (ca. 20–27 larvae L^{-1}). Tanks contained 275 L of seawater (18°–20°C) plus 100 L of a 1:1 mixture of the flagellate Tahitian *Isochrysis galbana* and the diatom *Chaetoceros gracilis* or *C. mulleri* Ehrenberg at a cell density of 2–4 × 10^6 cells mL^{-1}. In addition, lobster larvae received a supply of live, four day-old *Artemia* (initially 40–50 mL^{-1}) that were cultured and enriched at CMH.

Approximately 80 mL of dry brine shrimp eggs (Aquarium Products®, Glen Burnie, MD) were first decapsulated (Bruggerman et al. 1980) and then added to a 400-L conical tank containing only 100 L of filtered (1 μ) seawater (25°–29°C). After brine shrimp had hatched, the tank was filled with cultured algae (as above). After four days, the tank was drained and brine shrimp (ca. 3 mm) retained on a small sieve, the contents of which were added to one 400 L conical tank with larval lobsters.

Lobster larvae remained in the static culture tanks for two days before being transferred to an adjacent, clean tank containing vigorously aerated seawater, microalgae, and brine shrimp. The transfer process lasted no more than two minutes. We devised a dip net that was approximately 40 cm long × 30 cm wide × 20 cm deep made from nylon window screening. To transfer larvae, we would dip once from the larval tank and immediately empty the contents of the net into the clean tank. After six to seven dips, 95% of the larvae had been transferred. Next, we turned off the air and drained the seawater from the larval tank, quickly capturing the remaining larvae on a sieve (500 μ). This method also retained uneaten, live brine shrimp that also were added to the clean tank along with the lobster larvae. This transfer process continued for approximately two weeks, or until 85–90% of the surviving larvae had reached stage IV, when they were released to the wild. It never was necessary to add any antibiotics or other medication to a culture tank. From 1988–1992, survival rates from stage I to IV averaged 44%. These early benthic phase animals were released at depths of 10–20 m on or near cobble bottom in along a 170 km stretch of coast from Cutler (44°14′N, 67°27′W) to Tenant's Harbor (43°33′N, 69°03′W) Maine.

The larval culture techniques employed at CMH were different from methodologies that had been used to that date (Hughes et al. 1974; Serfling et al. 1974a; Schuur et al. 1976; Van Olst et al. 1980) primarily because of work conducted at the University of Maine's Darling Marine Center (DMC, Walpole, ME) from 1983-1985 by one of us (S. Chapman). Prior to the mid-1980's, most culture work on planktonic American lobsters was conducted in 40 L round-bottom, fiberglass tanks known as kreisels, planktokreisels, or "Hughes pots," after work published by John Hughes, former director of the Massachusetts State Lobster Hatchery (MSLH; Oak Bluffs, Martha's Vineyard, MA; Hughes et al. 1974) and his colleagues in California (Serfling 1974b; Ford et al. 1975; Van Olst et al. 1977). Highest estimated survival rates to stage IV per kreisel (35–85%) occurred when stage I larvae were stocked at densities between 500 and 3,000 (12.5–75 L^{-1}) and fed either live or frozen *Artemia* throughout the culture period (Hughes et al. 1974). Van Olst et al. (1980) reported that, "When food and larvae are uniformly distributed and proper densities of both are maintained, larval survival to stage IV will average 60–75%." Schuur et

TABLE 5.

ANOVA on the angular-transformed survival data from Experiment C (25 August).

Source of variation	df	Sum of squares	Mean square	F value	Pr > F
Density	2	61.28	30.64	6.58	0.0118
(50 vs. [100 & 150]/2)	1	53.02	53.02	11.39	0.0055
(100 vs.150)	1	8.26	8.26	1.77	0.2075
Food	1	27.88	27.88	5.99	0.0307
Density × food	2	6.86	3.43	0.74	0.4990
Error	12	55.87	4.66	—	—
Total	17	151.89	—	—	—

See Table 4 for description of food types. $n = 3$.

TABLE 6.

Percent survival (±95% CI) of larval lobsters in Experiment D (4–22 September 1986).

Density	Diet	Day 4	Day 6	Day 8	Day 10	Day 12	Day 14	Day 16	Day 18
25	*M. arenaria*	46.7 (20.69)	37.3 (15.18)	37.3 (15.18)	37.3 (15.18)	33.3 (11.51)	28.0 (17.21)	24.0 (9.94)	24.0 (9.94)
	S. scombrus	41.3 (50.02)	37.3 (50.02)	33.3 (59.89)	30.7 (54.73)	24.0 (57.74)	24.0 (57.74)	22.0 (49.25)	20.0 (42.75)
50	*M. arenaria*	38.0 (21.66)	31.3 (17.42)	31.3 (17.42)	28.0 (14.91)	24.0 (4.97)	24.7 (7.62)	20.0 (17.91)	20.0 (17.91)
	S. scombrus	36.0 (34.42)	25.3 (25.00)	25.3 (25.00)	23.3 (20.08)	20.0 (9.94)	17.3 (7.59)	13.3 (7.59)	12.0 (4.97)
100	*M. arenaria*	33.0 (11.40)	22.0 (13.83)	19.7 (15.97)	17.3 (21.13)	13.7 (13.68)	15.3 (21.13)	13.3 (14.98)	13.0 (14.90)
	S. scombrus	40.0 (2.48)	30.0 (7.46)	29.0 (6.57)	27.7 (6.25)	23.7 (1.44)	12.7 (11.74)	8.0 (11.38)	7.0 (12.91)

Density = number per 3.785 L. Aeration (High = 240 mL air sec^{-1}). Diet (6–8 mm pieces): soft-shell clam (*M. arenaria*) or mackeral (*Scomber scombrus*) in combination with four day-old, enriched live brine shrimp (*Artemia salina*). Day refers to days after hatching. $n = 3$.

al. (1976) reported that a maximum survival rate of 70% can be attained when 1500 larvae from a single day's hatch are added to a "Hughes pot" and are fed live brine shrimp over a two-week period at temperatures of 20.0 ± 0.5°C. Although a number of studies used these culture techniques (Hughes et al. 1974; Serfling et al. 1974a, Schuur et al. 1976), none indicated how final numbers of stage IV animals were counted, none provided estimates of mean survival or variability, and none described how larvae were handled prior to stocking each kreisel.

One of us (B. Beal) visited MSLH in November 1991. At that time, it was reported by staff that survival rates of larval lobsters from stages I to IV at MSLH typically were in the range of 15–20% and rates had been at those levels for many years (M. Syslo, director, MSLH, pers. com., 7 Nov. 1991). At that time, 40-L planktokreisels were being used as culture vessels and frozen brine shrimp used as a food source. Stocking densities of stage I larvae were estimated to be 2,000 per culture vessel.

Several published accounts from Canada suggest good success in rearing American lobsters from stage I–IV in planktokreisels (Aiken et al. 1981; Aiken and Waddy 1989; Aiken and Waddy 1995; Eagles et al. 1984; Waddy 1988; Waddy and Aiken 1998). Aiken and Waddy (1995) indicated that a diet of frozen brine shrimp will produce survival rates of 35–65%; however, Eagles et al. 1984 noted that these highly variable survival estimates were related to the quality of frozen brine shrimp. Waddy and Aiken (1998) reported that maximum stocking density of stage I larvae into 40 L kreisels at the St. Andrews Biological Station (St. Andrews, New Brunswick) was "50–75 larvae per liter" (2,000–3,000 per kreisel). Best survival rates occurred at 20°C when live adult brine shrimp were maintained at a ratio of four/lobster larvae. Although Waddy and Aiken (1998) gave no specific survival rates, they referred to Schuur et al. (1976) for a range of estimates from stage I to IV (60–75%).

According to Serfling et al. (1974a), a system to mass culture *Homarus americanus* larvae must: (1) provide water circulation enough so as to suspend both food and lobster larvae without eddies or still-water pockets; (2) use a filtration system that maintains a well-oxygenated and high water quality independent of the seawater source; (3) be operable on a fully-closed, recirculating basis for several weeks; (4) function without continuous surveillance and operate independent of outside electrical power and water supplies; (5) have temperature control; (6) have provisions for effective control of diseases; and (7) be relatively maintenance free, inexpensive, and easy to build. The system used at CMH and elsewhere (see below) was developed primarily to enable non-scientists working in non-academic or non-research settings to culture *H. americanus* larvae to stage IV. Although the culture parameters outlined by Serfling et al. (1974a) have been successful in some settings, they assume a degree of technical sophistication (especially the filtration and recirculating systems) that usually does not exist in the situations we have been working for the past two decades (i.e., with fishers and their family members).

Our culture approach uses large volumes of air to suspend and disperse both lobster larvae and food (live, enriched brine shrimp) inside large, 400-L cone-shaped tanks. These methods depend on clean seawater, and function well for two-day intervals before the entire system must be cleaned and larvae transferred to another tank. Because CMH was relatively small ($60m^2$), we found the most efficient method of keeping seawater temperature reasonably constant was to use an air conditioner. One of the most important

TABLE 7.

Percent of larvae at each stage on each sampling date for Experiment D.

			Percent in larval stage				Total	Total %
Day	Date	T°C	I	II	III	IV	Alive	Alive
1	4 Sept	20.0	100				1050	100.0
4	8 Sept	20.1		95	5		422	40.2
6	10 Sept	21.7		71	29		297	28.3
8	12 Sept	19.8		34	66		286	27.2
10	14 Sept	20.8		25	73	2	263	25.0
12	16 Sept	18.9		1	76	23	215	20.5
14	18 Sept	17.6			35	65	180	17.1
16	20 Sept	19.3			6	94	143	13.6
18	22 Sept	18.8			4	96	136	13.0

TABLE 8.

ANOVA on the angular-transformed survival data from Experiment D (22 September).

Source of variation	df	Sum of squares	Mean square	F value	Pr > F
Density	2	252.02	126.01	3.87	0.0533
(25 vs. [50 & 100]/2)	1	161.01	161.01	4.95	0.0480
(50 vs. 100)	1	91.01	91.01	2.80	0.1227
Food	1	117.46	117.46	3.61	0.0840
Density × food	2	4.19	2.09	0.06	0.9379
Error	11	358.01	32.54	—	—
Total	16	731.68	—	—	—

Refer to Table 6 for specific information about food type. $n = 3$.

pieces of information we discovered during our experimental trials that subsequently influenced our culture practices was in the timing of collection of the stage I larvae from the broodstock tank. We have been unable to find many specific references in the literature concerning this aspect of culturing lobsters. Aiken and Waddy (1995) state, "Hatching larvae are screened from the outflow of the maternal female's tank each evening and stocked in specially designed larval tanks (planktokreisels) that disperse water in an upward rotation that keeps the larvae in uniform suspension, reducing injury and cannibalism." Sastry (1975) and Chang and Conklin (1993) each describe a broodstock holding/larval collection system similar to those used at CMH in 1986. That is, filtered seawater flows unidirectionally into individual compartments holding egg-bearing females, which carries stage I lobsters into plexiglass catch baskets (no size given) with 1 mm mesh screening. "Each morning the removable catch baskets are examined for larvae, and, if present, the larvae are rinsed into a larval-rearing system" (Chang and Conklin 1993). Baskets facilitate the ease with which stage I larvae are collected and transferred to kreisels; however, we abandoned their use at CMH after 1986. We found both experimentally and in routine culture situations that, because of their cannibalistic tendencies, stage I larvae, if confined to small areas at high densities without *Artemia* or other food, either die immediately or become stressed or injured, resulting in high rates of mortality (i.e., > 50%) within the first week of culture (e.g., Experiments B–D). If capture or collection baskets were emptied often enough (i.e., before a critical density occurred within each), they would be useful. Instead, we opted to place 3–5 broodstock at a time in a small (1320 L), covered, static, lightly–aerated tank and collected larvae periodically (every 30–60 min) through the day using small, aquarium, fish nets. Stage I larvae hatched during the evening were not added to culture tanks at CMH; instead, they were liberated in a cove adjacent to the hatchery.

The culture methods outlined here are not specific to the American lobster. In 1992, a lobster (*Homarus gammarus*) stock enhancement effort was initiated in Ireland at the National University of Ireland, Galway Shellfish Research Laboratory (SRL) in Carna (53° 18′ N, 9° 49′ W). The system was based on using 40-L kreisels (Hughes et al. 1974) that were connected to a heated seawater reservoir system (18°C). Stage I larvae (density = 25–37 L^{-1}) were suspended by a continuous flow of recirculated seawater at 9 L min^{-1} and fed a combination of chopped mysid shrimp (*Neomysis* spp.), mussel (*Mytilus edulis* L.), and occasionally supplemented with live *Artemia*. After 17 days, survival rates were 9.8% (Browne 1999). In March 1993, the culture system was converted to one more closely resembling the one at CMH (Browne 1999; Beal, pers. obs.). Similar mass-to-number relationships were discovered for stage I *H. gammarus* larvae (Browne 1999) so that careful stocking estimates could be obtained. After 11–14 days in the hatchery, Browne and Mercer (1998) observed an average larval survival rate to stage IV of 47%.

The culture techniques used at SRL were transferred to a fishermen's cooperative lobster hatchery in southeast Ireland during the mid-1990's. In August 2000, one of us (B. Beal) visited this hatchery (Carne, County Wexford, Ireland) where lobsters have been produced for stock enhancement since 1994. The culture methods used are similar to those described by Browne and Mercer (1998) and Browne (1999). Stage I larvae are collected soon after release by the female and are placed into vigorously aerated seawater (18°–21°C) within 80 L conical tanks (hoppers) at densities

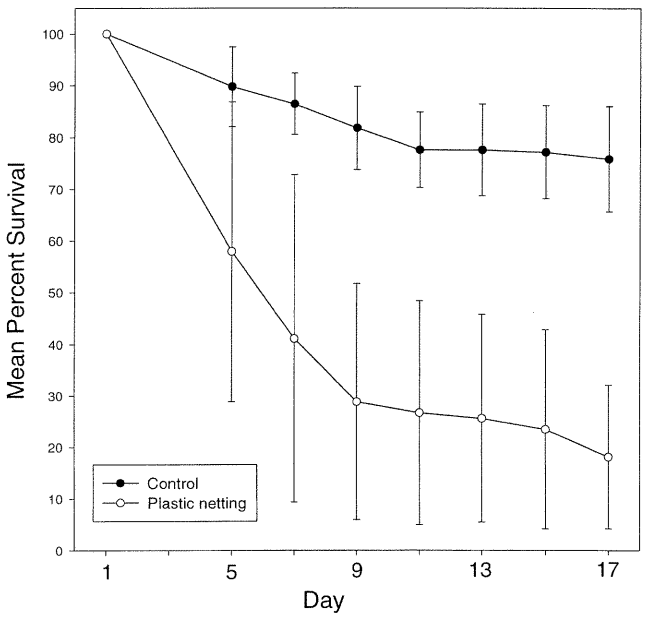

Figure 2. Experiment E. Mean percent survival ± 95% CI of *Homarus americanus* larvae through time for control (●) ($n = 6$) experimental units and those containing a piece of extruded, plastic netting (○) (6.4 mm aperture, $n = 5$). Larvae were stocked at 75 $unit^{-1}$ (ca. 20 L^{-1}), fed four day-old live brine shrimp and received vigorous aeration (i.e., 240 mL air sec^{-1}) during the entire experimental interval. Experiment was terminated on day 17 after 98% of larvae had metamorphosed to stage IV.

of 1500–2000/tank (19–25 L^{-1}). Tanks contained two species of cultured phytoplankton (Tahitian *Isochrysis galbana* and *Chaetoceros gracilis*) and live, algal-enriched brine shrimp. Larvae are transferred every second day to freshly prepared hoppers. Survival rates of lobster larvae from stage I to IV average 45% according to hatchery staff (N. Perrella, hatchery manager, pers. com., 24 August 2000).

Culture of *H. gammarus* for stock enhancement also took place in the United Kingdom in Wales and Scotland for nearly two decades beginning in 1973 (Beard et al. 1985, Lee and Wickins 1992, Wickins 1998). Larvae, stocked at 25 L^{-1} and fed twice daily with mysid shrimp (*Neomysis* spp.) and supplemented three times per week with newly hatched *Artemia* nauplii (Beard and Wickins 1992), were cultured in 100 L modified Hughes pots (planktokreisels) containing 80 L of seawater (16°–19°C). Flow rates of 7.5 to 12 L min^{-1} kept larvae and food suspended for the 11–17 days it took to reach stage IV. Survival rates (10–15%) of stage I to IV at the Ministry of Agriculture, Fisheries and Food's (MAFF) Fisheries Laboratory at Conway, North Wales were much lower than those reported from the two culture facilities in the Republic of Ireland (Beard et al. 1985, Beard and Wickins 1992). Similar survival rates were obtained at MAFF's Seafish Marine Farming Unit in Ardtoe, Scotland by Burton (1992).

The culture techniques described here are relatively simple, straightforward, and have withstood the test of time in a variety of hatch-and-release settings both in Maine (*Homarus americanus*) and Ireland (*H. gammarus*). Experiments A–D and the first year of production at CMH (1986) demonstrated that keeping lobster larvae and food well suspended within culture containers is important, but, without careful management of stage I larvae (i.e., collecting for culture within 30–60 min of release by the female), typical survival rates from stage I to IV will be less than 15%. Our techniques that produced a range of survival rates from 60% to 90% in the laboratory are not intended to replace those described elsewhere (Hughes et al. 1974, Serfling et al. 1974a, Van Olst et al. 1977, Aiken and Waddy 1989, Lee and Wickins 1992). These, too, have been used successfully in a number of disparate locations and production scenarios. Rather, we believe the culture methods described here provide another option for fishers, mariculturists, or research scientists to produce large numbers of stage IV clawed lobsters for stock enhancement, commercial enterprise, or experimental purposes.

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