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Survival and growth of hatchery-reared individuals of the European lobster, *Homarus gammarus* (L.), in field-based nursery cages on the Irish west coat

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Abstract

At present, one of two strategies is employed by fisheries managers for enhancing wild stocks of homarid lobsters using hatchery-reared individuals. The first is repeated releases of large numbers (>5000 at a time) of postlarvae (stage IV and V; carapace length [CL] = 5–7 mm) to selected bottom locations. This option exists primarily because these programs lack space, time, and/or the finances to rear animals to larger sizes that would most likely have initially higher survival rates. The second is to rear animals in the laboratory for 5–8 months to stage XII+ (CL = 12–16 mm) and then release small numbers (<1000) of these relatively large juveniles. To date there has been no attempt to release large numbers of relatively large juveniles because the costs are too prohibitive.We have developed a low-cost, low-maintenance, field-based nursery caging system for rearing cultured lobsters, *Homarus gammarus* (L). Individuals (780 and ranging in CL from 5.2 to 7.2 mm) were reared in pre-fouled and unfouled containers (360 cm^3) fabricated from an extruded plastic netting (3.2 mm aperture) and in pre-fouled plastic petri dishes (200 cm^3) that were deployed in five near-bottom cages for 10 months (September 2000 to June 2001) at two subtidal sites located in a shallow, relatively exposed embayment on the west coast of Ireland. Animals apparently were able to survive and grow by suspension feeding on the plankton and/or foraging on the fouling community that settled on and within individual containers. Mean recovery rate ($\pm$ 95% CI) was independent of a priori fouling treatments, but was site-specific (42.1 $\pm$ 7.9% and 27.8 $\pm$ 13.7%; $n = 5$). These rates are minimal estimates of survival because we found that at least 20% of the animals were capable of escaping from the mesh containers. Mean recovery in petri dishes that prohibited emigration was 53.3 $\pm$ 37.02% at one site and 75.0 $\pm$ 23.1% ($n = 5$) at the other. These recovery rates compare favorably with survival rates of fed conspecifics held in the laboratory over the same time (54/

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81 = 66.7%). At the end of the experiment, animals in field cages had mean CLs that were significantly smaller than the fed controls. Because of costs incurred with maintaining small lobsters under laboratory conditions, results of this short-term, manipulative field experiment indicate that field-based nurseries represent an economically viable, third option for managers of lobster stock enhancement programs.

Keywords: Field-based nurseries; Fouling community; *Homarus gammarus*; Ireland; Lobsters; Stock enhancement

1. Introduction

Stock enhancement, or ranching, of cultured clawed lobsters (*Homarus gammarus* [L.] and *H. americanus* Milne Edwards) has occurred in Europe and the United States, respectively, since the mid-1800s (Nicosia and Lavalli, 1999). Early attempts to increase lobster stocks by confining large numbers of ovigerous females in tidal impoundments where they release their stage I larvae into the water column (Rathbun, 1886) were never critically tested, but commercial landings did not increase noticeably in and around the release sites. Subsequent programs occurred to enhance European and North American stocks by rearing larvae in the laboratory through their three planktonic stages to produce large numbers of early benthic phase animals for direct release to the wild (Hughes et al., 1974; Van Olst et al., 1977; Beard et al., 1985; Bannister, 1998; Browne and Mercer, 1998; Wickins, 1998; Beal and Chapman, 2001); however, few field tests to investigate the efficacy of these "seeding" activities have taken place (but see Wahle and Incze, 1997; Bannister and Addison, 1998; Beal et al., 1998).

Numerous reasons have contributed to the difficulties of assessing the efficacy of lobster stock enhancement activities. These include lack of continued funding for public production facilities and monitoring/sampling programs (Beal et al., 1998), variable hatchery/laboratory survival of larvae and postlarvae leading to large interannual differences in numbers of juvenile lobsters released (Wickins, 1998), the relatively low numbers of animals released at any one site through time (Bannister et al., 1994), and poor economic returns (Bannister, 1998; Latrouite, 1998). In addition, the cryptic behavior of early benthic phase lobsters (Lawton and Lavalli, 1995) and high juvenile mortality rate presumably due to predation (Wahle and Steneck, 1991, 1992; van der Meeren, 2000) combined with enormous logistical constraints imposed by searching and sampling the benthos (Mercer et al., 2000) make it difficult to estimate the short-term success of stocking programs with much confidence. Also, longer-term studies of tagged lobsters (sensu Linnane and Mercer, 1998) are difficult to interpret because certain assumptions must be made about tag retention, emigration and catch rates, and the relationship between number of tagged individuals per sample, size of the sample, and actual number of tagged animals remaining alive in the larger population (Bannister, 1998).

Typically, stock enhancement programs use one of two strategies to release cultured juveniles. Some groups stock large numbers (>5000 per released) of small (stage IV or V) lobsters (Burton, 1992; Beal et al., 1998; Browne, 1999) primarily because of space and food limitations while others release relatively small numbers of larger animals ($\geq$ stage

VII) that have been held and fed in the hatchery for >3 months (Bannister and Addison, 1998; Scovacricchi et al., 1999; van der Meeren, 2000). Since predation risk decreases with increasing size in lobsters (Wahle, 1992; Lawton and Lavalli, 1995), a third strategy for managers might be to grow and release large numbers of larger animals. This tactic has not been adopted due to logistical and economic constraints. Although considerable work has occurred to develop economical culture systems for juvenile lobsters reared individually or communally in the laboratory (Chanley and Terry, 1974; Lang, 1975; Sastry, 1976; Van Olst and Carlberg, 1978; Kendall et al., 1982; Aiken and Waddy, 1988; Conklin and Chang, 1993), costs remain too expensive to provide adequate space and nutrition to rear large numbers of juvenile lobsters (>stage VII) for stock enhancement purposes (Bannister and Addison, 1998; but see Knudsen and Tveite, 1999). In Norway, van der Meeren (2000) suggested that if production costs exceeded 1£ (US$1.45) per released lobster juvenile (6 months to 1 year old), stock enhancement efforts were not cost-effective given losses of animals mainly due to bottom-feeding fish.

We developed and tested a field-based, nursery growout system for rearing post-larval juveniles of *H. gammarus* at a subtidal location along the west coast of Ireland from August 2000 to June 2001. Our hypothesis was that individual lobsters could survive and grow by feeding on nothing but suspended zooplankton (Lavalli and Barshaw, 1989; Barshaw, 1989) and/or grazing on organisms that fouled the small, plastic mesh cages that contained them. Here, we present results of field and laboratory experiments that suggest that managers of enhancement programs who choose to release stages IV–V lobsters due to space, nutritional, and/or economic limitations have another option. That is, they may now choose to grow juvenile lobsters in simple, inexpensive, field-based nursery cages and release larger animals that, presumably, have a better chance of survival compared to smaller individuals.

2. Materials and methods

2.1. Juvenile lobsters

A total of 1536 hatchery-reared European lobsters (stage IV, $n=184$; stage V, $n=830$; stage VI, $n=246$; stage VII, $n=276$) was obtained from the Wexford Lobstermen's Cooperative in Carne, County Wexford, Ireland on 24 August 2000 (seawater temperature = 17 °C). Animals were added to plastic trays (25 × 75 cm) divided into 192 individual compartments, placed into chilled styrofoam coolers, and transported 6 h to the National University of Ireland, Galway's Shellfish Research Laboratory (SRL) in Carna, Galway. Animals were immediately placed in ambient flowing seawater (19 °C). Approximately 6.6% of the 1536 animals did not survive the handling and transport. Mortality was independent of size class ($G=4.28$, $df=3$, $P=0.23$). Animals were maintained (fed ad libitum small, freeze dried krill and dead, fresh mysid shrimp [*Neomysis integer* {Leach}]) in the trays that were placed in shallow tanks receiving ambient seawater until they were added to individual mesh containers and deployed in the field and laboratory (see below). Only lobsters with both chelae were used in the experiments.

2.2. Containers—lobster tents and petri dishes

Two types of containers were used to individually house juvenile lobsters. Most (92%) of the 780 lobsters used in the field experiment ($\bar{x}_{\text{Carapace Length [CL]}} = 6.0 \pm 0.2$ mm, range = 5.2–7.2 mm CL, $n = 30$) were added to containers constructed of extruded, black plastic netting (3.2 mm aperture; InterNet, N. Minneapolis, MN, USA). Netting was cut initially in the form of a rectangle (21.6 × 28 cm). A square, with sides measuring 6.4 cm, was removed from each corner of the rectangle and then this cross-shaped polygon was folded into an elongated pyramid (approximate length of 13 cm, width of 5.5 cm, and height of 8.5 cm). Flexible, stainless steel rings were used to pinch together the sides and top of the container at two points approximately 8 cm apart. The sides of the container, hereafter referred to as a "lobster tent," were in contact with each other a distance of approximately 3.5 cm. This gave a living space for each lobster of approximately 360 cm^3 (13 × 5.5 × 5 cm).

One lobster was added to a tent by using fingers to apply a small force equally to each end. This force pushed apart the two sides creating a momentary 8-cm gap along the top of the tent that was large enough in which to carefully insert a small lobster. Lobsters were removed (lifted) from individual compartments within plastic trays using a flattened (15 mm wide) plastic stick and each gently transferred immediately to a tent. Once inside, the applied force was released and the tent returned to its original shape trapping the lobster within. Tents were placed in shallow tanks with ambient seawater until they were added to cages and deployed at the field sites (see below).

The remaining lobsters used in the field experiment were added to plastic petri dishes (10 cm diameter × 2.5 cm wide; 200 cm^3). Twenty-five holes (1.6 mm diameter) were drilled in the cover and bottom portion of each dish. Two rubber bands were used to secure each cover to its dish.

2.3. Laboratory handling experiment

To determine short-term effects of handling on lobster survival and whether tents actually retained lobsters, we conducted a laboratory experiment at SRL from 27 August to 3 September 2000. One lobster (stage V; size range = 5.5–6.2 mm CL) was placed into each of 20 tents and these were added to a shallow (20 cm deep) tank receiving ambient seawater.

2.4. Nursery field cages

Tents (72) and dishes (6) were added to each of ten vinyl-coated wire (4.0 mm diameter) cages (3.2 cm aperture) measuring 70 × 47 × 43 cm and weighing approximately 10 kg. Each cage was designed with eight equidistant, horizontal shelves (levels). Levels were accessible via a door (70 × 57 cm). Levels 2, 3, 4 and 6 each received 18 lobster tents (3 × 6 matrix) while six dishes were added to level 5 (3 × 2 matrix). Tents remained in their matrix positions on each shelf because adjacent tents in rows and columns were in direct contact with each other. When the cage door was tied shut, this forced the tents even closer. Each of the six petri dishes was tied securely to the fifth

shelf nylon twine. There was no room for additional dishes on the shelf. No tents or petri dishes were added to the topmost (1) and two bottommost (7 and 8) levels. In addition, we did not record the size (stage) of lobsters within particular tents and dishes and assumed that stage IV–VII individuals were evenly distributed between levels within each cage.

Before deploying cages in the field, we tied a 30 cm diameter, plastic, air-filled buoy to the top of each. The bottom of each cage was tied to an 80 kg anchor (tire filled with cement). A distance of 1 m existed between the anchor and cage so that when deployed, each would remain vertical (i.e., shelves horizontal to the seafloor) and off the bottom. A piece of rope was tied to each anchor and extended to the seawater surface via a small buoy that enabled us to retrieve and sample cages (see below). The nursery cage arrangement was similar to that shown in Beal et al. (1995; Fig. 2) for overwintering juveniles of the soft-shell clam, *Mya arenaria* L.

2.5. Study sites

Over the period 4–9 September 2000, five cages (390 lobsters) were placed at each of two subtidal locations (Finish Rocks and Rusheenyvulligan) within the relatively shallow waters of Mweenish Bay (53°18′ 12″N; 9°37′ 55″W), adjacent to the SRL. The nursery sites, which were approximately 1 km apart, were chosen specifically because they were the two deepest places in Mweenish Bay (A. O'Conghaile, personal observation.), and as such, we considered site a fixed factor in all statistical analyses (see below). Both sites were relatively exposed to swells, winds, and storms from the southwest; however, the Finish Rock site was closer to the mouth of the Bay, and therefore, experienced more severe weather than at Rusheenyvuligan (A. O'Conghaile, personal observation). The sea floor at each site was sandy with occasional outcrops of granite ledge covered with *Laminaria saccharina* (L.), *Saccorhiza polyschides* (Lightfoot) Batters, and occasional stands of *Ectocarpus* spp.

Average tidal range in Mweenish Bay is 3.5 m, and at low spring tides, water depth at one site (Finish Rocks) was 4.5 m and at the other (Rusheenyvulligan) was 5.5 m. Seawater temperatures in the Bay, as recorded from unfiltered, constantly flowing seawater within a shallow tank at the SRL, ranged from 4.5 (20 January 2001) to 17 °C (4 September 2000) (Fig. 1) during the experimental interval, which ended on 6–7 June 2001. Salinity in the Bay, recorded at the SRL with a LF 191 Conduktometer, ranged from 31 to 33 psu over the same period.

2.6. Experimental design and null hypotheses

The field experiment was designed to test whether small, hatchery-reared lobsters can survive in the field by feeding on organisms that foul the containers that house them. To test whether or not it was necessary to pre-foul the containers, we created two types of lobster tents—fouled and unfouled. Before pieces of netting were folded, 75% of the material was placed into a tidal pond at SRL approximately 45 days before manufacturing the tents. During this period, fouling organisms and algae settled onto the netting. Although not quantitatively examined, diatoms, spirorbid polychaete worms (ca. 1 mm),

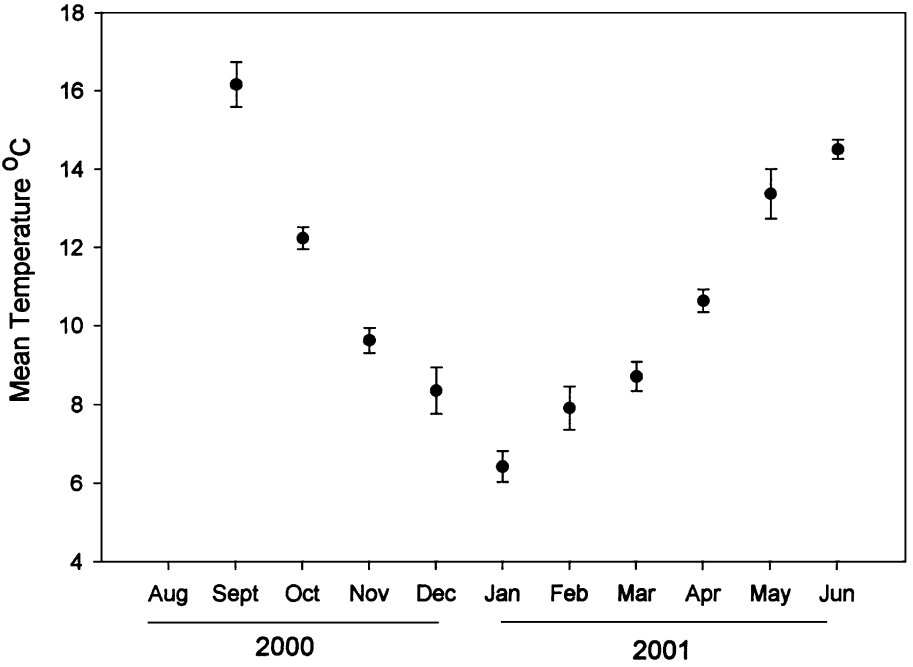


Fig. 1. Mean seawater temperature (± 1 SE) in Mweenish Bay Galway, Ireland as recorded at the Shellfish Research Laboratory in Carna.

small tunicates (< 2 mm), and strands (4–5 mm in length) of the green alga, *Enteromorpha intestinalis* (L.) Nees, were noted on most pieces of netting. None of the netting was fouled heavily as it was easy to discern all the apertures. All petri dishes were similarly fouled. Of the 72 tents added to each cage (4 levels of 18 tents), three levels contained fouled tents (2, 4, and 6) and one level (3) contained 18 unfouled tents.

We measured the mean percent of animals recovered from each level of each cage to test three null hypotheses:

(1) There are no differences between sites;
(2) There are no differences between levels. This hypothesis includes three sub-hypotheses, or contrasts:
   (a) mesh tents vs. plastic petri dishes (Levels 2, 3, 4, 6 vs. Level 5)
   (b) fouled vs. unfouled tents (Levels 2, 4, 6 vs. Level 3)
   (c) topmost vs. bottommost tents (Level 2 vs. Level 6);
(3) The effects due to level do not differ between sites.

2.7. Field sampling

Prior to our final sampling, we sampled three cages at random from both sites on three dates in 2000 (18 September, 2 October, 13 November) and one date in 2001 (12 March).

Cages were lifted from the bottom onto the deck of a research vessel and all pre-fouled tents (levels 2, 4, and 6) were sampled. All tents from each shelf were sampled by forcing open the 8-cm gap in the top of each tent and visually inspecting the inside. We recorded whether lobsters were alive, dead, or missing and then returned the tent back to its original position on the shelf. Sometimes, an animal was not readily visible because of intense fouling on the outside of the tent. In those cases, we placed the tent in a bucket of seawater and examined it (without pinching the ends) by turning it from one side to the other before we made a determination. No petri dishes were sampled. Cages were returned to the approximate location on the seafloor where they had been. The length of time to sample one cage was approximately 15 min.

2.8. Controls

We employed two types of controls—fed and unfed. Animals in the fed controls (81) were divided evenly into three size classes ($\bar{x}_{\text{Small}} = 5.8 \pm 0.19$ mm, range = 5.5–6.2 mm CL, $n = 5$; $\bar{x}_{\text{Medium}} = 6.6 \pm 0.09$ mm, range = 6.4–6.9 mm CL, $n = 5$; $\bar{x}_{\text{Large}} = 7.3 \pm 0.15$ mm, range = 7.0–7.8 mm CL, $n = 5$) and housed in an unheated, Quonset-style barn at SRL. Each group was placed into a separate plastic tray (30.5 × 91.4 cm) with twenty-seven 10.2 × 10.2 cm cubicles lined with fiberglass window screening (3 mm aperture) and the three trays placed into a single, shallow, aerated tank that received ambient, unfiltered seawater (ca. 4 l/min) from Mweenish Bay. Lobsters were fed ad libitum twice weekly from 1 September 2000 to 11 June 2001 with frozen *Neomysis* that were collected periodically from a saltwater pond adjacent to the SRL. We noted the date when a lobster shed or when it died. At the end of the experiment, the CL of all live animals was measured using a Nikon dissecting scope with ocular scale and the mass of each recorded to the nearest 0.0001 g using a Salter electronic balance (Model ER-182A).

A total of 264 animals was used in the unfed controls. Animals were either placed individually into fouled or unfouled tents (as described above) or unfouled 250 ml clear plastic soda bottles with 25 small holes (1.6 mm diameter) drilled into each Containers were placed into open, black, plastic shrimp culture boxes (41.0 × 32.5 × 12.7 cm) that were deployed in tandem (one on top of the other). Each box had a series of square holes (7.0 mm aperture) along the sides and bottom to allow sufficient exchange of water. The top of the upper box was covered with a piece of mesh netting (6.4 mm aperture) directly underneath which was a piece of styrofoam approximately 20 cm long × 15 cm wide × 3 cm thick. The top box nested within the bottom box and these were tied together. We attached a piece of twine approximately 25 cm long from the bottom box to a cement block (ca. 9 kg) so that when deployed, the two boxes would be lifted off the bottom. We deployed 17 pairs of boxes at four locations (Table 1). These extremely shallow (≤ 1 m) controls were sampled from 5 to 11 June 2001 and all live animals were counted, measured (CL), and the mass of each recorded as described above.

2.9. Statistical analyses

Analysis of variance (ANOVA) was used to test for differences in mean percent recovery between sites and levels. We tested the normality assumption using the Shapiro–

Table 1
Unfed lobster controls

Date deployed (2000)	Date sampled (2001)	Location	Pairs of boxes[a]	Fouled tents	Unfouled tents	Unfouled 250 ml bottles	Total number of lobsters
27 August	5 June	SRL[b]	2	16	8	–	24
28 August	5 June	SRL	2	16	8	–	24
1 September	5 June	SRL tidal pond[c]	4	32	16	–	48
4 September	11 June	Tidal pond east of SRL[d]	4	32	16	–	48
10 September	11 June	Tidal pond east of SRL	1	–	–	24	24
18 September	11 June	Tidal pond east of SRL	2	–	–	48	48
22 September	5 June	Tidal creek west of SRL[e]	2	–	–	48	48
Totals			17	96	48	120	264

[a] Each shrimp box held six tents or 12 bottles.
[b] Boxes were placed into aerated, 750-l tanks with ambient, flowing seawater in the Shellfish Research Laboratory.
[c] Two pairs of boxes were placed at the southern end where salinities were recorded as low as 18 psu; two pairs of boxes were placed at the northern end where salinities were 30–31 psu; water depth at both ends of the pond was <1 m.
[d] Site was 200 m from SRL; water depth at low tide was ca 1 m.
[e] Site was 400 m from SRL; water depth at low tide was ca 0.5 m.

Wilks test (SAS, 1988) and the assumption of variance homogeneity using Cochran's test (Winer et al., 1991). The percentage data were normal, but required an arcsine, or angular, transformation to homogenize the variances (Sokal and Rohlf, 1995). The field layout was a type of split-plot design (Steele and Torrie, 1980; Underwood, 1997), and as such, the analysis contains both factorial (crossed) as well as nested elements. We employed the following linear model

$$Y_{ijk} = \mu + A_i + B(A)_{j(i)} + C_k + AC_{ij} + BC(A)_{jk(i)}$$

where Y_{ijk} = mean transformed percent of lobsters recovered within each level of each cage, μ = theoretical mean, A_i = site (Finish vs. Rusheenyvulligan—fixed factor), B_j = cage (five cages within each site—random factor), C_k = Level (2, 3, 4, 5, 6 within each cage—fixed factor).

Because the experimental design contained no true replicates of experimental units (levels were not replicated within a given cage), it was not possible to test for cage (site) and level × cage (site) effects. Therefore, we assumed that there was no significant cage-to-cage variability within sites and that the variation from level to level was similar in all cages at both sites. The design did permit us to test several orthogonal, single degree-of-freedom a priori hypotheses related to container type and the effect of level on the dependent variable. These included:

1. tents vs. dishes;
2. fouled vs. unfouled tents;
3. uppermost vs. bottommost tents.

The first two contrasts are confounded with level; however, since tents were positioned both above and below the dishes within a cage, the confounding is likely to be unimportant. The same logic can be applied to the second contrast.

We used regression analysis to test equality of slopes of the untransformed mass–CL relationship to compare: (1) within and between fed and unfed controls, and (2) between fed controls and the animals in the field cages. When slopes were equivalent, we conducted an analysis of covariance (ANCOVA) to determine whether the separate lines had different intercepts or whether the lines were coincident.

3. Results

3.1. Handling experiment (27 August to 3 September 2000)

Live lobsters were recovered from 16 of 20 tents (80%). It is presumed that animals in four tents somehow escaped from the tank via the overflow pipe as none were recovered.

3.2. Fed controls

Mean survival ($\pm$ 95% CI) of lobsters in the fed controls pooled across each of the three initial sizes (66.7 $\pm$ 11.77%, $n=3$) was relatively high during the 284-day experiment. Most (ca. 80%) of the mortality occurred within the first 60 days and no lobsters deaths were recorded in any of the three groups after 30 January 2001. Final survival rates for the small, medium, and large lobsters were 74%, 66.7%, and 59.3%, respectively. More than 60% of the deaths occurred within a period of 3–5 days after ecdysis. ANOVA indicated that molting frequency was size-specific ($F=3.21$, $df=2$, 51, $P=0.0451$) as animals in the smallest size category molted significantly fewer times (2.4 $\pm$ 0.28, $n=20$) than larger lobsters (3.2 $\pm$ 0.16, $n=16$). Final CL, however, was not significantly different between the three groups (mean CL = 11.7 $\pm$ 0.14 mm, $n=54$; $F=2.56$, $df=2$, 51, $P=0.0875$), indicating the possibility of compensatory growth in these animals. We found no differences in the slopes ($F=0.01$, $df=2$, 48, $P=0.9915$) or intercepts ($F=0.47$, $df=2$, 50, $P=0.6280$) of the mass–CL relationship (Mass [g] = $-1.39+0.196$ CL [mm]; $r=0.95$, $n=54$, $P<0.0001$) between the three groups suggesting that animals were morphologically similar. The color of the animals, especially immediately after molting, was a pale blue similar to that described by Browne (1999). The color of these animals tended to darken between molts, but was still primarily blue.

3.3. Unfed controls

Mean survival of animals in the unfed controls pooled across all locations (Table 1) was low (13/264 or 4.9%). No lobsters survived in boxes at the tidal creek or the tidal pond east of the SRL, and none were recovered alive in any of the 250 ml bottles ($N=120$) or in any of the unfouled tents ($N=48$). Six of the animals recovered alive resided in the shrimp boxes floating inside the 750-l tanks within the SRL while the remaining seven lobsters were found within boxes in the high salinity end of the SRL tidal pond. There was a

significant difference in mean CL ($P = 0.0164$) and mean mass ($P = 0.0422$) between the two locations as lobsters in the SRL tidal pond were approximately 20% longer (9.7 ± 0.19 vs. 8.1 ± 0.66 mm) and 45% heavier (0.50 ± 0.04 vs. 0.35 ± 0.05 g) than those held inside in tanks within the SRL. Mean CL and mass of both groups was, however, significantly smaller and lighter, respectively, than the "Small" animals in the fed controls ($P < 0.0001$), although animals from the SRL tidal pond had the same mass–CL relationship as the fed controls ($F = 0.26$, $df = 2, 58$, $P = 0.6148$). The slope of the mass–CL relationship for animals held in tanks within the SRL was significantly different (lower) from that of the fed controls ($F = 12.39$, $df = 1, 55$, $P = 0.0009$).

3.4. Field experiment

We observed a steady decline in percent of lobsters recovered from the pre-fouled tents during the four preliminary samplings (Fig. 2). Noteworthy is the fact that only 83.3% and 76.7% of the animals were recovered at Finish Rocks and Rusheenyvulligan, respectively, on the first sampling date (ca. 2 weeks after the experiment was initiated). In addition, it appeared that relatively high losses occurred between the November 2000 and March 2001 sampling, when only 36.1% of the animals were recovered at Finish Rocks and 50% at Rusheenyvulligan. These samples can be used only to estimate relative losses through time and do not provide a complete picture of events within the nursery cages because none of the unfouled tents and dishes was inspected.

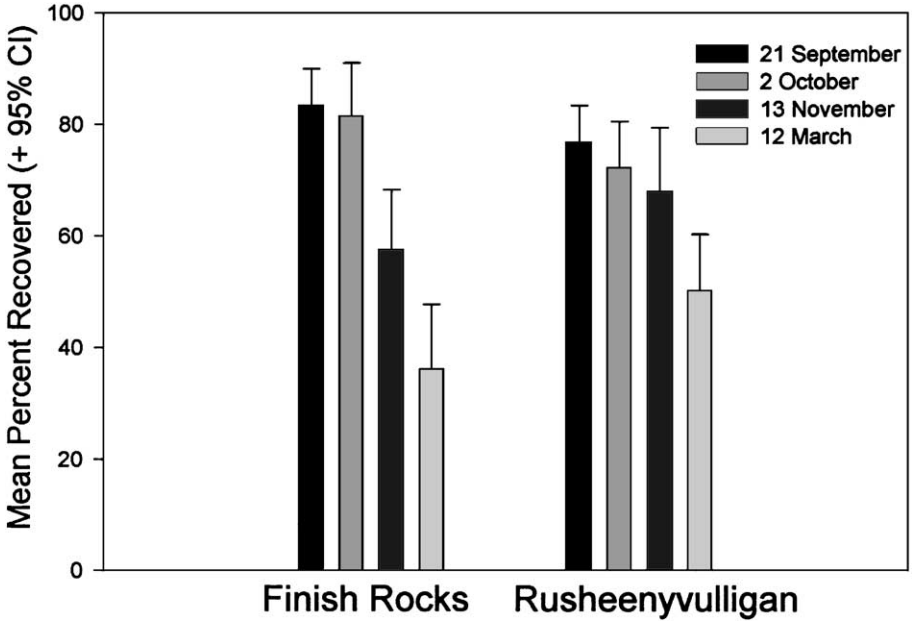


Fig. 2. Mean percent of juvenile European lobsters recovered in pre-fouled tents in each of three randomly sampled cages at two sites in Mweenish Bay for three sampling dates in 2000 and one in 2001. Animals were placed in the field cages from 4 to 9 September 2000.

Table 2
ANOVA results on the arcsine-transformed percent recovery data of juvenile European lobsters reared in cages in Mweenish Bay, County Galway, Ireland from 4–9 September 2000 to 6–7 June 2001

Source of variation[a]	*df*	SS	MS	*F*	Pr>*F*
Site	1	1533.41	1533.41	7.75	0.0238
Cage (site)	8	1583.50	197.94	–	–
Level	4	5364.67	1341.17	9.66	0.0001
(1) Tents vs. dishes	1	4987.36	4987.36	35.94	0.0001
(2) Fouled vs. unfouled tents	1	87.73	87.73	0.63	0.4324
(3) Top vs. bottom tents	1	199.87	199.87	1.44	0.2389
Site × level	4	1124.00	281.00	2.02	0.1145
Cage × level (site)	32	4440.69	138.77	–	–

Sites (Finish Rocks and Rusheenyvulligan) and levels within each cage were considered fixed factors while cage was considered a random factor. An adjusted type I error rate (α') of 0.01695 was used for each of the three single degree-of-freedom orthogonal contrasts.

[a] MS cage (site) used as an error term for hypothesis test involving site effects and MS cage × level (site) used as an error term for hypothesis tests involving level and site × level effects (after Underwood, 1997).

Final mean percent (± 95% CI) recovered on 6–7 June 2001 was 42.1 ± 7.9% ($n=5$) and 27.8 ± 13.7% ($n=5$) from Finish Rocks and Rusheenyvulligan, respectively. ANOVA indicated that this site difference was significant ($P=0.0238$; Table 2). In addition, there was a highly significant effect due to level ($P<0.0001$) that was consistent between sites

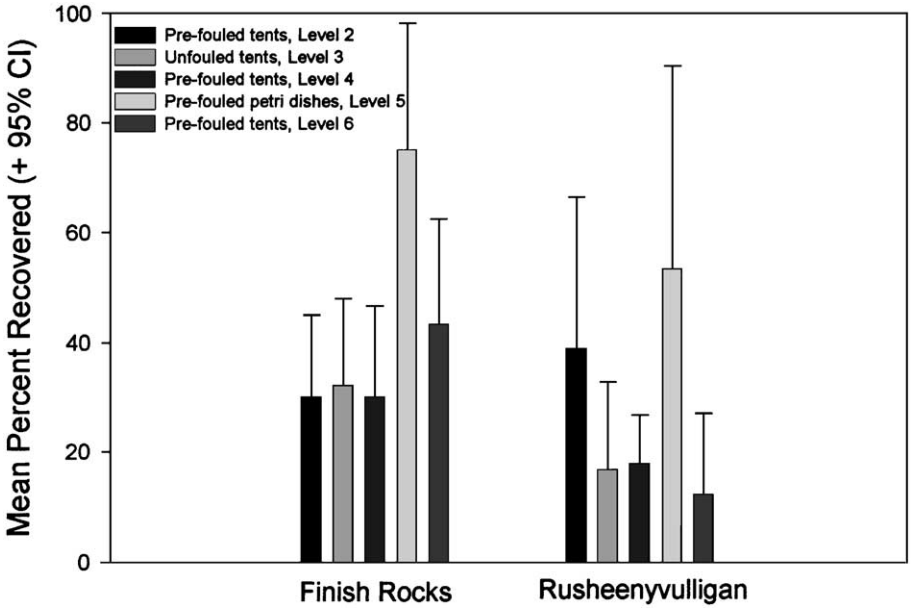


Fig. 3. Mean percent of juvenile European lobsters recovered from field cages at two subtidal sites located in Mweenish Bay on 6–7 June 2001. ANOVA indicated that significantly more animals were recovered from Finish Rocks than Rusheenyvulligan ($P=0.0238$) and that recovery rates were more than double in petri dishes than in tents ($P<0.0001$, $n=5$).

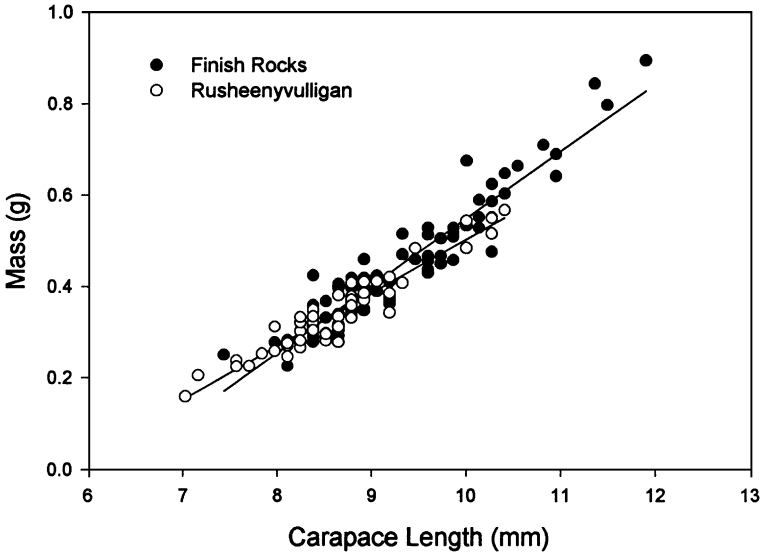
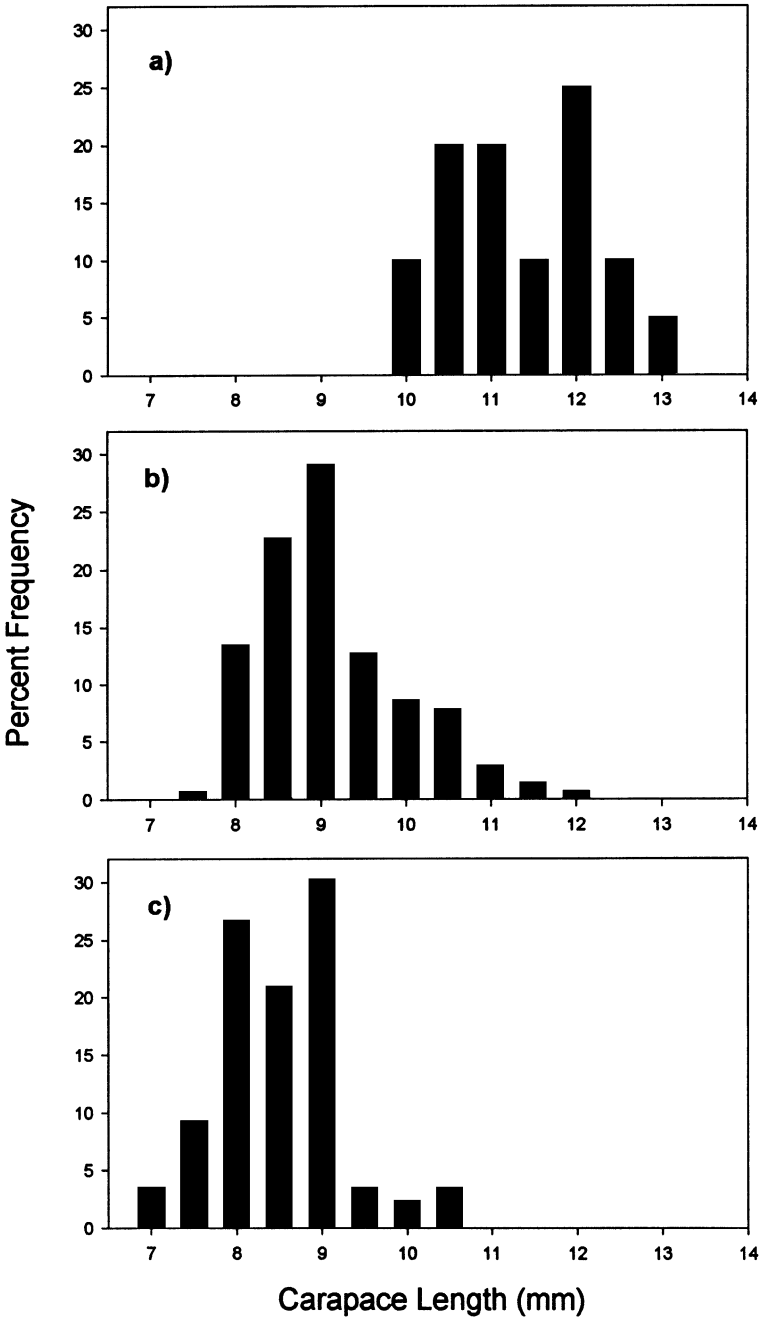


Fig. 4. Relationship between CL and mass of juvenile European lobster from the field cages at two subtidal sites in Mweenish Bay. Regression analysis indicated that the slopes of the lines were not equal ($P=0.0007$). Finish Rocks: mass (g) $= -0.93 + 0.147 \times$ CL (mm) ($r=0.948$; $n=83$; $P<0.0001$). Rusheenyvulligan: mass (g) $= -0.66 + 0.117 \times$ CL (mm) ($r=0.951$; $n=53$; $P<0.0001$).

($P=0.1145$). Most (92.9%) of the variability associated with the level source of variation was due to the difference in recovery rates of juvenile lobsters between petri dishes and tents (both fouled and unfouled; orthogonal contrast #1 from Table 2; Fig. 3). Mean percent recovered from petri dishes pooled across sites and cages was $64.2 \pm 18.6\%$ ($n=10$) compared with $27.6 \pm 7.4\%$ ($n=10$) from the tents. Neither of the two other contrasts was significant ($P>0.20$), which suggest that pre-fouling of containers was not important prior to establishing juveniles in field nurseries and that percent recovery was independent of level within the cages (Table 2). The color of the animals, independent of site, level within a cage, or type of container varied from brown to reddish brown with white mottling on the carapace, chelae, and telson. We did not observe a single animal from the field that resembled the blue color of animals within the fed controls.

The carapace, chelae, and tail of a large percent of the animals recovered at both sites were fouled with the polychaete, *Spirorbis spirorbis* (L.) (41/143 or 28.6% and 28/93 or 30.1% at Finish Rocks and Rusheenyvulligan, respectively, but none of the animals within the dishes at either site was fouled). These animals, along with a small number of animals that had lost one or both chelae or had unequal chelae, were not included in the regression analysis to determine if the mass–CL relationship differed between sites. This test

Fig. 5. Final size frequency distribution of European lobsters. (a) "Small" fed controls ($\bar{x}=11.4 \pm 0.40$ mm, $n=20$); (b) and (c) represent animals from field cages at Finish Rocks ($\bar{x}=9.1 \pm 0.14$ mm, $n=143$) and Rusheenyvulligan ($\bar{x}=8.6 \pm 0.15$ mm, $n=93$), respectively. ANOVA and SNK demonstrated that the three means were significantly different ($P<0.0001$).


a)
b)
c)
Percent Frequency
Carapace Length (mm)
0
5
10
15
20
25
30
7
8
9
10
11
12
13
14

demonstrated that the slopes of the lines were not equal ($F = 11.95$, $df = 1, 132$, $P = 0.0007$; Fig. 4). Since it was not possible to examine lines from both sites together, we asked whether the mass–CL relationship varied from level to level at both sites. In both cases, the slopes of the lines were equal ($P > 0.35$) and there was no effect due to level ($P > 0.35$).

To determine whether lobster grew differently in the field vs. the laboratory, we compared the mass–CL relationship of the fed controls to that of the unfouled, morphologically complete animals in the nursery containers. The slopes of the lines (fed vs. Finish Rock lobsters and fed vs. Rusheenyvulligan lobsters) were not equal, and in both cases, were steeper for the fed vs. field animals. Mean CL of the smallest animals in the fed controls (11.4 ± 0.40 mm, $n = 20$) was 25% greater than that of animals held in cages at Finish Rocks (9.1 ± 0.14 mm, $n = 143$) and 33% larger than those at Rusheenyvulligan (8.6 ± 0.15 mm, $n = 93$) (Fig. 5). ANOVA indicated that mean CL differed significantly ($F = 190.61$, $df = 2, 254$, $P < 0.0001$) between the three groups and the a posteriori Student–Neumann–Keuls (SNK) test revealed that all three means were significantly different. In addition, we tested whether mean CL was affected by level within the cages ($F = 1.53$, $df = 4,32$, $P = 0.2173$) and whether or not the interaction of site and level was significant ($F = 1.89$, $df = 4, 32$, $P = 0.1387$).

4. Discussion

Our results provide an unambiguous answer to the question of whether it is possible to rear and grow hatchery-reared juveniles of *H. gammarus* in field-based nurseries without feeding or otherwise maintaining the animals or the structures that house them. Our 10-month field experiment at two shallow sites in a relatively exposed embayment on the Irish west coast was conducted during the stormiest and coldest time of the year; yet, animals survived and grew in their individual containers. Although the combined mean percent of lobsters recovered from both sites was only $34.9 \pm 8.1\%$ ($n = 10$), we regard this as a minimal estimate of survival for two reasons. First, our weeklong laboratory experiment demonstrated that animals were able to escape from the handmade, plastic mesh tents. It is likely that escape rates were higher at the two field sites where tidal currents, storm surges, and other abiotic factors were capable of physically moving through the water column the cages that were securely tethered to the bottom. Second, as many as $75 \pm 23.1\%$ ($n = 5$) of the animals were recovered alive in the petri dishes (Fig. 3), where it was nearly impossible for lobsters to escape. Covers of these dishes were tightly secured with two rubber bands and then the entire dish was tied solidly in place to the shelf/level on which it rested. Since recovery rates of lobsters held in dishes were significantly higher than rates from plastic tents at both sites (Table 2), we conclude that many of the animals not confined to dishes simply crawled to freedom through small gaps or other openings in the tents presumably caused by imperfect folding of the plastic netting or insufficient pinching of the stainless steel rings to create a sufficient seal between the top and sides of some tents.

At least three alternative hypotheses may explain differences in recovery rates between dishes and tents: differential fouling, handling, and mortality. First, although we did not measure quantitatively the degree of fouling that occurred on/in dishes and tents, we did

not notice a difference in the fouling community that developed these two types of containers. At the end of the experiment, when all containers were examined, dishes and tents at both sites were fouled with a similar array of organisms (amphipods, barnacles, bivalves, spirorbids, and tunicates). Second, neither dishes nor the unfouled tents were inspected on the four occasions when cages were sampled randomly (Fig. 2). Had recovery rates been similar between these two types of containers, handling (removing and inspecting tents) may have helped to explain the observed differences. They were not (Fig. 3). Once cages were brought on the deck of the research vessel, seawater drained completely from the tents and dishes, which remained in this state for up to 15 min. This handling apparently did not affect recovery rates. Third, it is possible that cumulative stress from being confined to crawling and molting on an uneven, extremely rugose surface (mesh netting) resulted in higher mortality rates of lobsters in the tents compared to animals restricted to the relatively smooth and even surface the dishes afforded. Although we did not test this hypothesis directly, final mean CL did not vary significantly between levels (and, therefore, between tents and dishes) at either site. Differential mortality could also have been due to predators. Porcellanid crabs (*Pisidia longicornis* [L.]) were observed in several tents, however, none were observed in any of the dishes.

Lobsters in field cages grew more slowly (25–33%) and differently than animals fed frozen mysids in the laboratory. While we were unable to conduct an ANCOVA on the mass–CL relationship between the fed controls and animals in the nursery cages, the slopes of the lines indicated that mass increased at a greater rate per unit CL for animals in the laboratory. One explanation for this difference in growth rate could be seawater temperature. From 1 September 2000 to 1 April 2001, "Small," fed, control lobsters molted, on average 0.90 ± 0.38 times ($n = 20$). Seawater temperatures during most of this period were below 10 °C (Fig. 1). Between 1 April and 11 June 2001 those same animals molted 1.5 ± 0.18 times ($n = 20$) as mean seawater temperatures in the laboratory reached >14 °C. Temperatures in the laboratory during the spring, however, were probably warmer than seawater at the field sites for several reasons. First, the intake pipe at the SRL was moved in October 2000 so that seawater was being pumped from near the surface of Mweenish Bay where temperature are, on average, warmer than they are at either of the field sites (D. Brown, technician, SRL, personal communication, 7 June 2001). Second, the tanks holding the fed controls were shallow and the depth of water in cubicle varied from 3 to 6 cm. Residence time for water in the tank varied from 10 to 15 min, depending on tidal height. Tanks were located in a Quonset-style barn with a series of translucent ceiling panels that resulted in elevated air temperatures compared to outside temperatures, especially during sunny days. Together, these conditions combined to increase seawater temperatures in the laboratory compared to the field. On two occasions (1 and 7 June 2001), one of us (B. Beal) measured seawater temperature at high tide at a pier near the intake pipe at the SRL and in the shallow tank holding the control animals. Temperatures were 0.5 and 1.0 °C warmer in the laboratory on the first and second date, respectively. Since molting frequency in homarids is related directly to seawater temperature (Van Olst et al., 1980), it is likely that thermal conditions experienced by the fed control animals were cumulatively higher than those in the field.

Two alternative hypotheses may explain differences in lobster growth between the field and the laboratory: nutrition and the presence of predators. No assessment was made of the

nutritional value of mysid shrimp compared to organisms that fouled the containers; however, it is possible that animals grew faster in the laboratory because their consistent diet of shrimp required minimal energy to search and handle prey. It is likely that until cages became completely colonized by fouling organisms, lobsters in field cages spent considerable time searching for food. Lastly, the presence of predators, especially during post-molt periods, may have limited the time lobsters in field cages spent searching and handling food.

Our data also indicate the site-specific nature of field-based nurseries. Both field locations were deeper than any other sites in Mweenish Bay, and other than a 1-m difference in water depth between them, the sites were physically very similar. Before the final sampling, we would have predicted recovery rates at Finish Rocks should be lower than at Rusheenyvulligan because that site was shallower and closer to the mouth of the Bay. Contrary to that prediction, however, recovery rates were nearly 15% greater at Finish Rocks ($P < 0.025$; Table 2). Since fouling rates were similar between sites, we offer no remarkable explanation for the observed differences. Conversely, it is clear why recovery rates in the field cages were higher than rates in the unfed controls that were placed within and adjacent to the SRL (Table 1). Those sites were extremely shallow (≤ 1 m) and the fouling community was relatively undeveloped compared to the deeper water sites. That is, we observed few amphipods, bivalves, tunicates, and polychaetes on or within the tents and bottles at the end of the experiment. In addition, these containers holding the unfed controls often were filled with sediments, which was not observed at the Mweenish Bay sites. This and other observations suggest that the environments where we placed the controls were very different from the deeper water sites. Furthermore, salinities in the tidal creek and in the SRL tidal pond were lower than those recorded from Mweenish Bay. On two occasions, when we recorded salinities in the tidal pond and tidal creek (21 October 2000 and 14 April 2001), we observed levels as low as 18 psu. Although these salinities are within the tolerance range of homarids (Van Olst et al., 1980), it is likely that the interactive effect of low salinities, relatively high silt loads, and extreme temperatures stressed the animals causing their deaths.

Our results contribute to the debate on diets of postlarval and juvenile lobsters (Juinio and Cobb, 1992; Lawton and Lavalli, 1995). Animals in both pre-fouled and fouled containers were able to survive and grow by foraging on organisms that either were captured directly from the water column (suspension feeding) and/or that settled and grew on the surfaces of the containers (raptorial feeding). Barshaw (1989) and Lavalli (1991) demonstrated that postlarvae and early juveniles of the American lobster were able to survive and grow on diets of barnacle nauplii, copepods, crab zoeae, and unidentified zooplankton (< 1 mm). Jatzke (1970) showed it was possible to rear early juveniles of *H. gammarus* in the laboratory for up to 17 months on a natural diet of plankton, small crustaceans, coelenterates, and polychaetes. Although it was not a particularly strong test, our results suggest that *H. gammarus* are able to suspension feed (sensu Lawton and Lavalli, 1995). We found no significant difference in recovery rates between fouled and unfouled tents (Table 2, Fig. 3), but both types of containers were heavily fouled at the end of the experiment. Unfouled lobster tents were placed on a shelf within each cage that was sandwiched between shelves of pre-fouled tents. It is possible that food particles from these fouled tents could have settled into the unfouled tents and provided nourishment for

those animals during at least the first weeks of the field trial. It has been suggested that adults of the European lobster can suspension feed (Loo et al., 1993); however, since there has been no success in locating wild or planted postlarval or early juveniles of *H. gammarus* in the field over its geographic range (Linnane et al., 2000; Mercer et al., 2000), this study represents the first work to suggest that these small lobsters are capable of surviving and growing by forgoing on the plankton and fouling community.

Our results strongly suggest that field-based nurseries for postlarvae of *H. gammarus* can be used in conjunction with stock enhancement efforts. Currently animals either are released to the benthos soon after reaching stage IV or V (Browne, 1999) or are maintained individually in the laboratory for several months to attain larger sizes prior to their release. There have been no successful attempts to test the efficacy of hatch-and-release efforts using postlarvae of European lobsters; therefore, it is impossible to know precisely whether these efforts are effective. It is known that these small animals disperse quickly, and it is presumed they seek refuge in deep shelters that may be inaccessible to normal sampling gear (Mercer et al., 2000). It is also likely that many are preyed on soon after they are released on or near the bottom as occurs with postlarvae of *H. americanus* (Wahle and Steneck, 1992). In Norway, fish (mainly wrasses in the family Labridae) are responsible for substantial losses of early juveniles of *H. gammarus* (CL = 12–15 mm) within hours of their release on the bottom, especially during summer months (van der Meeren, 2000). Bannister and Addison (1998) concluded that historic release rates of cultured, stage XII+ European lobsters in the UK, France, Norway, and Ireland were too low and their recapture rates at commercial sizes were insufficient to justify the costs of ranching programs, except in areas where there is clear evidence of recruitment failure. This assessment was based, however, on costs associated with rearing animals in the laboratory that may take as many as 8 months to attain sizes of 15 mm CL (van der Meeren, 2000).

A complete economic analysis of field- vs. laboratory-based nurseries is beyond the scope of this study. However, several simple calculations indicate the cost effectiveness of using field cages to rear lobster postlarvae for stock enhancement programs. For example, the most expensive items in the present study were the vinyl-coated wire cages (US$45 each), lobsters (US$0.55–0.85, depending on size), and the petri dishes (ca. US$0.10). It is likely that some cost-savings in equipment can be found, but the cost of the cages, in particular, can be spread across many years because of their durability and longevity. (We observed no structural damage to any of the field cages over the 10-month field experiment.) Using a conservative estimate of 100 animals per container, we estimate the initial cost, excluding labor, to place 20,000 stage V in nursery field containers to be US$28,000 (200 cages @ US$45 each + 20,000 animals @ US$0.85 each + 20,000 containers @ US$0.10 each). This cost would be approximately US$19,000 in succeeding years because cages could be reused. Using the labor invested by one of us (B. Beal) to load lobsters into containers, place containers in the 10 cages, and deploy them in the field (24 h), we estimate the time to deploy 20,000 animals would be 480 h. Total equipment and labor costs (US$15/h) for the initial year would be US$35,200 (US$1.76 per lobster) and US$26,200 (US$1.31 per lobster) in subsequent years. Conversely, to rear only 5000 lobsters (US$4250) in a laboratory for a year (minimum of 16 h of labor per week = US$12,480), excluding expenditures of electricity and/or fuel, rent, equipment,

etc., would cost US$16,730 (US$3.35 per lobster) or, conservatively, nearly twice the amount (initial year) of placing lobsters in nursery cages. Since survival in the nursery is both container- and site-specific, future investigations should focus on determining the most cost-effective containment device as well as most suitable environment/habitat to rear animals.

We are aware of only one other published attempt to rear postlarval European lobsters in the field without any attention or care. Knudsen and Tveite (1999) conducted a 3-month experiment (summer to early fall) in a fjord near the Flødevigen Marine Research Station, His, Norway, using in situ cages deployed directly on the bottom with animals similar in size to those used in this study. They observed 100% mortality in cages that became covered with decaying macroalgae and/or drifting sand, but obtained a 66% overall survival rate. They observed no growth rate differences between field and laboratory (fed) animals and presumed lobsters in field cages were feeding on benthic meiofauna and small macrofauna. Although no mention is made in that study about exoskeleton color, we observed dramatic differences in coloration between the fed control groups (pale to dark blue depending on molt cycle) and animals reared in field cages (brown to reddish brown).

In addition, we have anecdotal observations suggesting that the color of animals in the field cages is more similar to the coloration of similar size animals in the wild. At times in the recent past, communal rearing experiments with hatchery-reared *H. gammarus* postlarvae have been conducted at the SRL (Browne, 1999; Linnane et al., 2000). Months after the experiments have been concluded and tanks cleaned that have received only unfiltered, ambient seawater from Mweenish Bay, we have discovered ca. seven individual lobsters that apparently escaped previous attempts to locate them (B. Beal and A. O'Conghaile, personal observation). None of these lobsters, hidden in the interstices of cobble and in lengths of black PVC pipe, appeared blue. Rather, the animals were dark brown, appearing more similar in color to the lobsters in our field cages. It is unclear whether predators of small European lobsters, such as fish and crabs, respond to variations in prey color, or whether antipredator lobster behavior and exoskeleton color are correlated. Laboratory studies with cultured, postlarval color variants of *H. americanus* (Beal et al., 1998) suggest that some predators (*Pseudopleuronectes americanus* [Walbaum], *Carcinus maenas* [L], *Myoxocephalus octodecemspinosus* [Mitchill]) do not respond to lobster colormorphs and that lobsters behavior is independent of exoskeletal color, but similar studies have yet to be conducted with *H. gammarus*.

The short-term nature of this study did not permit us to investigate the natural limits on growth or survival that may be imposed by this specific type of culture system. Future efforts should focus on determining maximum size of animals that can be attained in field-based nurseries. Ultimately, this work could provide fisheries managers and others engaged in stock enhancement efforts with information that may lead to cost-effective ranching programs (sensu Bannister and Addison, 1998). In addition, it may be possible to rear cultured juveniles in these low-cost, low-maintenance field nurseries to sizes well below those of the commercial fishery (i.e., 200–250 g), but still of interest to consumers familiar with other small crustaceans such as the Norway lobster, *Nephrops norvegicus* (L.) or cultured freshwater crayfish, *Procambrus clarkii* Latreille. Because *H. gammarus* is an attractive culture prospect due to its high value, demand, and worldwide market, the development of an entirely cultured product may be feasible. Finally, efforts continue

along the coast of Maine, USA, to stock hatchery-reared individuals of *H. americanus* (Beal and Chapman, 2001). Whether the techniques presented here are transferable to rearing American lobsters remains to be tested.

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