Survival of laboratory-reared juvenile European lobster (Homarus gammarus) from three brood sources in southwestern Norway


Published in:
New Zealand Journal of Marine and Freshwater Research

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

General rights
Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.
Survival of laboratory-reared juvenile European lobster (Homarus gammarus) from three brood sources in southwestern Norway

K.E. JØRSTAD
T.S. KRISTIANSEN
E. FARESTVEIT
A.-L. AGNALT
Institute of Marine Research
Bergen, Norway
email: knut.joerstad@imr.no

P.A. PRODÖHL
M. HUGHES
A. FERGUSON
School of Biological Sciences
Queen’s University Belfast
Belfast BT7 1NN
Northern Ireland, United Kingdom

J.B. TAGGERT
Institute of Aquaculture
University of Stirling
Stirling FK9 4LA, United Kingdom

Abstract Experiments were carried out from June 2000 to April 2001 to compare survival of European lobster (Homarus gammarus) offspring (larvae and juveniles) from three brood sources, Kvitsøy Wild (KW), Kvitsøy Cultured (KC), and Rogaland Wild (RW), Norway. In the first set of experiments, newly hatched larvae (stage I) were raised in separate family tanks. All larvae groups survived to stage III/IV, although large variation in relative survival was observed among families within each of the three different female groups. Highest overall survival was observed for the RW group (12.8%), whereas no differences in overall survival were found between the KW (9.0%) and KC groups (9.6%). From stage III/IV, larvae from single family tank experiments were mixed in five “common garden” juvenile experiments. These lasted for 9 months, and the surviving juveniles were identified to family/female group using microsatellite DNA profiling. Significantly higher survival of the KW families (7.0%) was found compared with the KC (3.7%) and the RW families (3.2%), and differences in family ranking of relative survival values were evident between the KW and KC groups. The relative survival rate of the different groups was independent of female lobster size. An estimate based on only stage IV larvae reduced the difference in survival between the KW (11.4%) and KC (8.3%) group. The experiments provided evidence that cultured females (KC) are producing viable offspring with lower, but comparable survival to that of offspring from wild females (KW).

Keywords common garden experiments; ranching; offspring survival; microsatellite DNA profiling; individual identification; family identification

INTRODUCTION

During the last decades, reported landings of European lobster (Homarus gammarus; Linnaeus 1758) in Norway have declined substantially from previous levels (Agnalt et al. 1999). Before the 1960s, annual landings ranged from 600 to 1000 tonnes and current registered landings are between 30 and 60 tonnes, indicating a decline of more than 90% (Agnalt et al. 1999, 2007). Stock enhancement experiments in Europe have been evaluated by Bannister & Addison (1998) and, in an attempt to develop new methods, a large-scale lobster enhancement experiment was initiated in 1990 in Norway to assess if releases of hatchery-produced juveniles can stabilise recruitment and hence increase stock on a long-term basis (Agnalt et al. 1999). Kvitsøy Islands in southwestern Norway were chosen for this release experiment partly because the islands are renowned for historically high lobster catches (Agnalt et al. 2004). In addition, the islands are separated from surrounding areas by deep-sea trenches that could
limit out-of-area movement by lobster. Nevertheless, lobster landings at Kvitsøy Islands were extremely low in the early 1990s in comparison with past catches, and there were indications of a long-lasting failure in recruitment (Agnalt et al. 2004).

For the hatchery production of the juveniles, wild berried females (i.e., carrying fertilised eggs) were collected from the local Kvitsøy fishery (Agnalt et al. 1999). Since previous releases of stage IV larvae in the United States and Canada have shown poor results (Nicosia & Lavalli 1999), the juveniles were raised in hatchery facilities for 9 months and released around Kvitsøy Islands when they reached sizes between 30 and 40 mm total length. Between 1990 and 1994, c. 128 000 hatchery-produced juveniles were released within the region (Agnalt et al. 1999). Before release, the juveniles were microtagged to allow their subsequent identification in local catches. Uglem & Grimsen (1995) reported tagging mortality between 1 and 4%, and a tag loss of c. 10% after 3 months, which is in accordance with previously reported values (Wickins et al. 1986). From 1995 onwards, more than 95% of all lobsters legally caught around the islands were assessed for the presence of a microtag. During the period between 1997 and 2001, previously cultured lobsters comprised 50 to 60% of all lobster captured (Agnalt et al. 2004). Furthermore, a specific number of the recaptured females of cultured origin were egg-bearing (Agnalt et al. 2004, 2007). Recent studies showed that these females matured at the same size and produced the same quantity and quality (dry weight) of eggs as wild females from the same area (Agnalt et al. 2007; Agnalt 2008).

In the hatchery, juveniles were reared in separate small plastic compartments until they were released at between 8 to 9 months of age (Grimsen et al. 1987). Thus, under this artificial environment, unpredictable selection factors are likely to be introduced, which could potentially cause genetic changes and/or changes in morphology and behaviour that could affect fitness (for details see Allendorf & Ryman 1987; Busack & Currens 1995). Potential genetic problems (genetic changes causing reduction in fitness under natural conditions, inbreeding, genetic drift) in connection with aquaculture-based hatchery operations have been discussed elsewhere (Allendorf & Ryman 1987; Busack & Currens 1995; Campton 1995; Staples 1999; Ferguson et al. 2007), setting guidelines to minimise undesirable genetic changes (Kapuscinski & Jacobsen 1987; Pepper & Crim 1996). One specific genetic concern is that interbreeding between wild and escaped farmed individuals or those deliberately released in stock enhancement and ranching programmes could result in reduced overall fitness and productivity in wild populations (Utter et al. 1993; Utter 2000). A decrease in overall lifetime fitness has been demonstrated in several experiments involving farm strains of Atlantic salmon, Salmo salar (Fleming & Einum 1997; McGinnity et al. 1997, 2003; Fleming et al. 2000).

Agnalt et al. (1999, 2004) showed that hatchery-reared lobsters contribute significantly to the local fishery at Kvitsøy, and thus demonstrate the potential of rebuilding depleted local stocks using hatchery approaches. Furthermore, the significant fraction of berried females of cultured origin in the commercial landings also indicates that these individuals reproduce successfully. However, the long-term success is largely dependent on the viability or fitness of the offspring from parents of cultured origin compared with that from wild parents. Direct comparisons of survival (fitness) of offspring produced from parents from different brood sources are best carried out in a communal “common garden” experiment (Conover & Present 1990; Ferguson et al. 1995) where offspring are mixed and tested under identical environmental conditions, thus eliminating environmental variability. Any differences found are thus the result of genetic and/or maternal influences.

The development of microsatellite primers for European lobster (Prodöhl et al. unpubl. data) provided required DNA markers that allow the identification of parentage of lobster individuals in these mixed experiments. Jørstad et al. (2005) applied these DNA identification methods to compare early larval survival from stage I to stage IV from wild and cultured berried lobsters, reared in mixed family tanks. Their findings showed a reduction (60%) in relative fitness in offspring of cultured females compared with that of offspring from wild females (Jørstad et al. 2005). In this study, we extended the observation period from stage III/IV to juveniles of approximately 9 months of age in a series of communal common garden experiments and estimated juvenile survival from three brood sources in southwestern Norway.

MATERIAL AND METHODS

All experiments were conducted in cooperation with the Kvitsøy Lobster Hatchery on Kvitsøy Islands in southwestern Norway. Details about the experimental design including collection of berried females, size

60 New Zealand Journal of Marine and Freshwater Research, 2009, Vol. 43
distributions, and hatching facility are described in detail by Jørstad et al. (2005). Briefly, several hundred berried females, from wild and cultured origins were collected from the commercial fishery in the Kvitsøy area (59°04′N; 05°25′E) between October 1999 and May 2000. Cultured females were identified based on the presence of coded wire tags. To include a reference broodstock, wild berried females were collected from a close-by region (12 km) in Rogaland (59°08′N; 05°35′E). All broodstock were individual tagged (Streamer tag, Hallprint Ltd, Australia), and sorted according to source as Kvitsøy Wild (KW), Kvitsøy Cultured (KC) and Rogaland Wild (RW). The females from KW ranged in sizes from 88 mm to 112 mm carapace length (CL), from KC—82 to 112 mm CL, and from RW—84 to 128 mm CL (Jørstad et al. 2005).

Production of single family stage III/IV larvae
Berried females of the three sources were kept in individual hatching units and the newly hatched stage I larvae were counted daily. Approximately 500 newly hatched larvae (hatched within the same 12 h period) were collected from single female hatching tanks and transferred to 20-litre single family incubators and then raised to stage III/IV. Owing to the differences in hatching time, it was necessary to carry out four different single family productions of stage III/IV larvae (Production 1–4), providing a total of 60 families (Table 1).

Each production period comprised tanks containing larvae from females that hatched within the same timeframe. Owing to the extended hatching period, offspring from one female of culture origin were used in two productions (Production 1 and 2, Table 1). Owing to an unpredicted high incidence of mortalities (probably caused by cannibalism) in all single family tanks, the separate rearing period was shortened to ensure sufficient numbers of larvae for the mixed tank juvenile experiments. Thus at transfer to common garden juvenile tanks and lobster park enclosures, the larvae consisted mostly of stage IV larvae, but stage III larvae were also included in the release. From each female used in the experiments, a biopsy of one walking leg was taken, and samples of eggs were collected and stored in 99% molecular grade ethanol for subsequent DNA extraction and microsatellite DNA profiling.

Common garden experiments
The larvae from the different single family productions (see Table 1) were counted and total length (TL; to the nearest 1 mm) measured. The larvae from each production (same age) were separately mixed and five juvenile common garden experiments were initiated. Two experiments were conducted in small meshed netting enclosures established on the sea floor in a lobster holding park

Table 1  Survival of newly hatched lobster larvae (stage I) to stage III/IV in single family tanks in four different productions (Production 1–4). Each production consisted of stage I larvae from different females and female groups hatching on the same day. Origin of females: KW, Kvitsøy Wild; KC, Kvitsøy Cultured; RW, Rogaland Wild, Norway. The survival index for each group was estimated as the ratio between the numbers of observed and expected survivors.

<table>
<thead>
<tr>
<th>Production</th>
<th>Brood source</th>
<th>No. of families</th>
<th>No. of released stage I</th>
<th>No. of observed stage III/IV</th>
<th>Survival %</th>
<th>Survival index</th>
<th>P (G-test) all</th>
<th>P (G-test ) KW × KC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>KW</td>
<td>4</td>
<td>1918</td>
<td>161</td>
<td>8.4</td>
<td>0.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>6</td>
<td>2641</td>
<td>344</td>
<td>13.0</td>
<td>1.28</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>4</td>
<td>1679</td>
<td>129</td>
<td>7.7</td>
<td>0.76</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2</td>
<td>KW</td>
<td>5</td>
<td>2493</td>
<td>349</td>
<td>14.0</td>
<td>0.97</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>4</td>
<td>2000</td>
<td>259</td>
<td>13.0</td>
<td>.900</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>6</td>
<td>3000</td>
<td>471</td>
<td>15.7</td>
<td>1.09</td>
<td>0.02</td>
<td>0.31</td>
</tr>
<tr>
<td>3</td>
<td>KW</td>
<td>8</td>
<td>3821</td>
<td>391</td>
<td>10.2</td>
<td>0.91</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>10</td>
<td>4725</td>
<td>479</td>
<td>10.1</td>
<td>1.07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>KW</td>
<td>6</td>
<td>3000</td>
<td>115</td>
<td>3.8</td>
<td>1.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>7</td>
<td>3500</td>
<td>158</td>
<td>4.5</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All productions</td>
<td>KW</td>
<td>23</td>
<td>11232</td>
<td>1016</td>
<td>9.0</td>
<td>0.91</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>27</td>
<td>12866</td>
<td>1240</td>
<td>9.6</td>
<td>0.97</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>10</td>
<td>4679</td>
<td>600</td>
<td>12.8</td>
<td>1.29</td>
<td>&lt;0.0001</td>
<td>0.35</td>
</tr>
</tbody>
</table>
facility (Park PA and Park PB). The enclosures were 12 m$^2$ (3 m × 4 m) and placed at 2.0 to 2.5 m depth in the lobster park. In PA, a total of 1079 larvae or 90.0 larvae per m$^2$ were released originating from Production 2 (Table 2). In PB, a total of 870 larvae were released or 72.5 larvae per m$^2$, originating from Production 3. Three experiments were conducted in three separate fibreglass tanks (1 m × 1 m) of water depths of c. 1 m; hatchery HA, HB, and HC (Table 2). Larvae from Production 1 were divided in two approximately equal numbers and released in HA and HB, at densities of 313 and 319 per m$^2$, respectively. 273 larvae were released in HC, all originating from Production 4. The natural larval density of European lobster is unknown (Mercer et al. 2001), and therefore the experimental densities in this study were based on survival estimates from earlier studies, as described in Jørstad et al. 2001. In total, 2854 stage III/IV larvae were released into the different rearing experiments during the period from 13 July to 11 August 2000.

In all experimental units (park and hatchery), the bottom substrate and shelters were similar, consisting of shell sand covered with empty scallops and oyster shells (Jørstad et al. 2001). Initially, juvenile lobsters were fed frozen Mysidae, whereas later stages were also fed small, frozen krill (predominantly *Meganypathanes norwegica*) and fish. Experiments lasted for c. 9 months, and the sampling of tanks (HA, HB, and HC) in the hatchery and in the lobster park facility (PA and PB) was carried out in April 2001. All lobster juveniles were collected, TL (to the nearest 1 mm) recorded and then stored in 99% molecular grade ethanol for subsequent DNA extraction and microsatellite DNA profiling.

### Juvenile identification to family and broodstock group

DNA extraction and subsequent genetic screening for six microsatellite marker loci on a Li-Cor automated genotyper followed standard procedures as described previously (Jørstad et al. 2005). Particular care was taken to include adequate control samples in each run (i.e., samples of known genotypes) to ensure data quality and consistency of typing. For each family belonging to the three broodstock sources (KW, KC, and RW) used in the experiments, the male contribution was established by subtracting the observed maternal contribution from each larval multilocus genotype. Only single male fertilisations were found. With information of the genetic makeup of each family, individual juvenile lobster from the five experimental groups were assigned to family and group by the exclusion principle, using the Family Analysis Program (FAP; Taggart 2007). In total, 148 juveniles were sampled and 12 juveniles could not be reliably assigned to group, mainly owing to poor DNA quality.

Following individual assignment, survival estimates were calculated as follows: the expected survival for each group and family was based on the average survival rate for each of the juvenile rearing units. The survival index for each group was estimated as the ratio between observed and expected survival (Jørstad et al. 2005). *G*-tests (with Williams correction; Sokal & Rohlf 1995) were used to compare survival rates of the three offspring groups (all families within groups pooled) in the five experiments with a significance level of 5% ($\alpha = 0.05$).

### Table 2  Summary statistics of the juvenile lobster experiments.

For each of the productions in single larval tanks (Production 1–4), stage III/IV larvae of the same age produced were mixed and five juvenile “common garden” experiments initiated. All experimental units (3 hatchery tanks—HA, HB and HC; 2 bottom enclosures in lobster holding park—PA and PB) were covered with bottom substrate and shelters. TL, total length in mm; % 2 claws, fraction of juveniles with 2 claws.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Production</th>
<th>Released stage III/IV</th>
<th>No. of juveniles</th>
<th>% survival</th>
<th>Mean TL (±SD)</th>
<th>% 2 claws</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery HA</td>
<td>1</td>
<td>313</td>
<td>15</td>
<td>4.8</td>
<td>29.1±5.2</td>
<td>33.3</td>
</tr>
<tr>
<td>Hatchery HB</td>
<td>1</td>
<td>319</td>
<td>22</td>
<td>6.9</td>
<td>26.9±3.6</td>
<td>54.5</td>
</tr>
<tr>
<td>Hatchery HC</td>
<td>4</td>
<td>273</td>
<td>17</td>
<td>6.2</td>
<td>25.3±4.6</td>
<td>64.7</td>
</tr>
<tr>
<td>Park PA</td>
<td>2</td>
<td>1079</td>
<td>36</td>
<td>3.3</td>
<td>30.4±6.4</td>
<td>49.1</td>
</tr>
<tr>
<td>Park PB</td>
<td>3</td>
<td>870</td>
<td>58</td>
<td>6.7</td>
<td>28.0±5.1</td>
<td>63.9</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2854</td>
<td>148</td>
<td>5.2</td>
<td>28.2±5.4</td>
<td>53.7</td>
</tr>
</tbody>
</table>
RESULTS

Survival to larval stage III/IV in separate family tanks

In the Production 1 experiment, the KC group had a significantly higher survival compared with the KW and RW groups, whereas the RW group had highest survival in the Production 2 experiment (Table 1). In three of the production cycles, there were no significant differences in survival indices between the KW and KC groups. When pooling all families from all experiments, the RW group had the highest overall survival (12.8%; survival index = 1.29). No differences were found between the KW (9.0%; survival index = 0.91) and the KC (9.6%; survival index = 0.97) group.

All family groups in the four production cycles (Production 1–4) had surviving stage III/IV larvae with the relative survival indices ranging from 0.26 to 1.90. The offspring from the cultured female had similar survival indices in the two productions, 1.2 in Production 1 and 0.76 in Production 2. The 60 families from all 4 experiments were ranked according to their relative survival indices, and showed similar rank distributions for each broodstock group (Fig. 1).

Juvenile survival in common garden experiments

The juvenile survival experiments covered the period from the first benthic stage (stage IV) to a juvenile size assumed suitable for either release purposes or farming under hatchery conditions. Overall survival in the units over 9 months was low (5.2%) across the five experimental units (Table 2). Survival in the different units ranged from 3.3% to 6.9%. Mean TL in the 5 units ranged from 25.3 ± 4.5 mm (SD) to 30.4 ± 6.4 mm, with an overall mean of 28.2 ± 5.4 mm. The fraction of lobster juveniles that had two claws at termination of the experiments, ranged from 33.3% to 64.7% with no apparent relation to density at release or at the end of the experiment.

Following the identification of the surviving juveniles to family and groups using microsatellite DNA profiling, the survival (%) and the survival index (observed/expected) of each group in the different common garden experiments were estimated. Significant differences were found in three of the experimental units (PB, HA, and HC) mainly owing to the higher survival of offspring of the KW families (Table 3). Thus, in these three experimental units, the survival indices were remarkably higher (PB—1.67; HA—1.71; HC—1.68, than the corresponding values (PB—0.45; HA—0.37; HC—0.51) for the KC group. The estimate for the RW families in HA was 1.86.

In contrast to the single family larval experiments (Production 1–4), 22 families had no surviving juveniles in the common garden experiments (KW, 7 families; KC, 11 families; RW, 4 families) suggesting high levels of competition under mixed family conditions. For the KW group, 69% of all families had survivors after 9 months, whereas the estimates for KC and RW groups were 59%
and 60%, respectively. There were differences in survival between the offspring from the KW and KC groups (Fig. 2), where the families within the three broodstock groups were ranked according to the overall ranking of their survival indices. Considering only families with surviving offspring at the end of the experiments, 75% of the KW group had a survival index >1.0 compared with 50% for the KC group. Overall survival based on the total number of stage III/IV larvae used (pooled data from all experiments; Table 3) of the KW group was 7%, whereas the corresponding value for the KC group was 3.8%, and 3.2% for the RW group. Larvae from one cultured female, with extended hatching, was used in three of the juvenile experiments (HA, HB, and PA), but none of them survived.

Survival indices for stage III/IV larvae and juvenile families were compared with female size (CL) for the three broodstock sources. There was no indication that a larger female was associated with higher survival of larval and juvenile stages compared with a smaller female for any of the broodstock sources investigated (Fig. 3). The size of female associated with no juvenile survival covered almost the entire size range.

The fraction of stage IV larvae varied in the different single tank families, which could influence survival rate in the juvenile common garden experiments. When repeating the overall analyses based on stage IV larvae only, the nominal survival rate for juveniles from the two wild broodstocks (KW—11.6%; RW—13.5%) was higher compared with that of the KC group (8.4%), although there were no significant differences (Table 3). These analyses were based on the assumption that none of stage III larvae would survive, but c. 60% of families with no survivors had a significant fraction of stage IV larvae, whereas c. 50% of families with only stage III larvae had survivors. Stage III larvae possibly moulted shortly after initiation of the experiments into stage IV larvae.

**DISCUSSION**

In the single-family units (Production 1–4), the overall survival of the RW group was higher compared with that of the KW and RC groups. No overall significant differences in survival were, however, observed during the early developmental

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Brood source</th>
<th>No. of released stage III/IV</th>
<th>No. of observed juveniles</th>
<th>No. of expected juveniles</th>
<th>Survival %</th>
<th>Survival index</th>
<th>P (G-test) all</th>
<th>P (G-test) KW × KC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery HA</td>
<td>KW</td>
<td>80</td>
<td>7</td>
<td>4.1</td>
<td>8.8</td>
<td>1.71</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>170</td>
<td>3</td>
<td>8.7</td>
<td>1.8</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>63</td>
<td>6</td>
<td>3.2</td>
<td>9.5</td>
<td>1.86</td>
<td>0.011</td>
<td>0.012</td>
</tr>
<tr>
<td>Hatchery HB</td>
<td>KW</td>
<td>81</td>
<td>4</td>
<td>5.1</td>
<td>4.9</td>
<td>0.79</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>173</td>
<td>14</td>
<td>10.9</td>
<td>8.1</td>
<td>1.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>65</td>
<td>2</td>
<td>4.1</td>
<td>3.1</td>
<td>0.49</td>
<td>0.281</td>
<td>0.350</td>
</tr>
<tr>
<td>Hatchery HC</td>
<td>KW</td>
<td>115</td>
<td>12</td>
<td>3.6</td>
<td>10.4</td>
<td>1.68</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>158</td>
<td>5</td>
<td>5.9</td>
<td>3.2</td>
<td>0.51</td>
<td>0.014</td>
<td></td>
</tr>
<tr>
<td>Park PA</td>
<td>KW</td>
<td>349</td>
<td>12</td>
<td>11.3</td>
<td>3.4</td>
<td>1.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>259</td>
<td>12</td>
<td>8.4</td>
<td>4.6</td>
<td>1.43</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>471</td>
<td>11</td>
<td>15.3</td>
<td>2.3</td>
<td>0.72</td>
<td>0.240</td>
<td>0.457</td>
</tr>
<tr>
<td>Park PB</td>
<td>KW</td>
<td>391</td>
<td>36</td>
<td>21.6</td>
<td>9.2</td>
<td>1.67</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>479</td>
<td>12</td>
<td>26.4</td>
<td>2.5</td>
<td>0.45</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>All experiments</td>
<td>KW</td>
<td>1016</td>
<td>71</td>
<td>48.4</td>
<td>7.0</td>
<td>1.47</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>1239</td>
<td>46</td>
<td>59.0</td>
<td>3.7</td>
<td>0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>599</td>
<td>19</td>
<td>28.5</td>
<td>3.2</td>
<td>0.67</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>All experiments</td>
<td>KW</td>
<td>612</td>
<td>71</td>
<td>63.9</td>
<td>11.6</td>
<td>1.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>KC</td>
<td>549</td>
<td>46</td>
<td>57.3</td>
<td>8.4</td>
<td>0.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>RW</td>
<td>141</td>
<td>19</td>
<td>14.7</td>
<td>13.5</td>
<td>1.29</td>
<td>0.091</td>
<td>0.079</td>
</tr>
</tbody>
</table>

Table 3 Survival of stage III/IV lobster larvae to juveniles (9 months) in communal rearing systems. All experimental units (hatchery tanks—HA, HB and HC; bottom enclosures in lobster holding park—PA and PB) were covered with bottom substrate and shelters. Origin of females: KW, Kvitsøy Wild; KC, Kvitsøy Cultured; RW, Rogaland Wild, Norway. The survival index for each group was estimated as the ratio between the numbers of observed and expected survivors.
Fig. 2  Ranking of family groups based on survival index estimated from juvenile survival after 9 months in “common garden” experiments, with origin of females from: A, Kvitsøy Wild; B, Kvitsøy Cultured; and C, Rogaland Wild, Norway. Individual juveniles were assigned to family group by DNA profiling; data from all experiments were pooled, and families were ranked across brood source.

Fig. 3  Survival index (crosses) of stage III/IV lobster larvae raised in single family units and juvenile survival index (open triangles) at c. 9 months of age related to female size (carapace length, CL) from different brood sources: A, Kvitsøy Wild; B, Kvitsøy Cultured; and C, Rogaland Wild, Norway.

stages (stage I to stage III/IV) between offspring from KW and KC brood sources. In one instance (Production 1), the survival of the KC group was found to be significantly higher than that of the KW group. Thus, the performance of cultured offspring under the conditions used was comparable to that of offspring of wild origin.

All the five juvenile experiments were characterised by an unexpected low overall survival (3.3%–6.9; Table 2) in comparison with earlier juvenile experiments using the same experimental approach (Jørstad et al. 2001). These previous experiments, however, were based on single families, or involved few families in mixture. Large family variation in survival (10–40%) in the previous experiments (Jørstad et al. 2001) and the size range (23–28 mm TL) in the present study are comparable
to observations in similar experiments carried out with American lobster, *Homarus americanus* (Van Olst et al. 1980; Aiken & Waddy 1995). The low overall survival observed in the present study suggests a high level of competition among the families and groups, which is also supported by the relative low frequency (53.7%) of juveniles with 2 claws (Table 2).

The first comparison of overall survival of juveniles from the three brood sources was based on the number of stage III/IV larvae produced in single family tank that suggested higher survival for the KW group (7.0%) compared with KC (3.7%) and RW (3.2%) groups. This difference was not because of variation in broodstock size (see Fig. 3), but could have possibly been influenced by the number of stage IV larvae. In the most conservative approach, assuming that none of the larvae released at stage III would survive, the KW group had still higher survival (11.6%) than the KC group (8.3%), but the difference was not significant. Under this assumption, the offspring (juveniles) from the three brood sources seemed to perform similarly under the experimental conditions investigated, but this assumption is incorrect since families with only stage III larvae had survivors and no survivors were found in families with a significant fraction of stage IV larvae.

The females of cultured origin are able to reach maturity, reproduce and produce viable eggs under natural conditions (Agnalt et al. 2004; Agnalt 2008). Our experiments, comparing survival of offspring from both wild and cultured berried females, demonstrate both successful hatching of larvae and survival of juveniles from each group under the environmental conditions used. Although little information is currently available about the early juvenile stages of *H. gammarus* (Mercer et al. 2001), juvenile density in our experiments was possibly markedly higher compared with natural conditions, which would mean high competition for shelter and food. In our experiments, only 53.7% of juveniles had two claws (Table 2), which was considerably lower than observed in earlier experiments (Jørstad et al. 2001) and possibly owing to higher initial larval density. Our hatchery experiments were free from predators and, thus, performance experiments in the presence of predators still need to be carried out. Predators might increase differential selection as reported by Petersson & Järvi (2006), observing differences in anti-predator response among native wild, native ranched and hybrid brown trout, *Salmo trutta*. Even short periods in culture may reduce the fitness under natural spawning conditions, as shown by several studies on sea-ranched Pacific salmonids (Reisenbichler & Rubin 1999). In a comparison of wild sea trout and a sea-ranched strain derived from the same stock, Petersson & Järvi (1997) found significant differences in mating behaviour. Releases could reduce the fitness of the wild population, especially if hybrids between ranched and wild individuals also show reduced survival. Potential effects of different forms of cultivation have recently been discussed in detail for Atlantic salmon, *Salmo salar* (Cross et al. 2007).

Both the KW and KC brood source originated from the local population in the Kvitsøy region. Except for the hatchery period of the KC group (reared for 9 months under artificial conditions and then released into the wild), the females experienced the same natural environment at Kvitsøy, possibly for 6–8 years before they reached maturity. The overall recapture rate of the hatchery-produced juveniles that were released at Kvitsøy was only about 6% (Agnalt et al. 2004). The berried females that were recaptured in the fishery and used as broodstock in the experiments described here, represent the most successful individuals in the large scale enhancement operation. The presence of cultured berried females in the fishery at Kvitsøy with similar fecundity as wild females (Agnalt et al. 2007) provides evidence for successful lobster stock enhancement. The long-term influence on the wild lobster population, including reproduction success of the cultured individuals and impacts on future lobster generations, is unknown and should be investigated.

**ACKNOWLEDGMENTS**

The experiments were part of GEL (Genetics of European Lobster) with financial support from EC FAIR CT98 4266. We are indebted to Einar Nøstvold at Kvitsøy Lobster Hatchery, Kvitsøy, Norway, for use of the hatchery facilities and close cooperation during this study. Directorate of Fisheries, Bergen, provided financial support for the collection of berried females from the Kvitsøy lobster fishery, and these were fundamental for the experiments conducted. We are also indebted to valuable suggestions from two reviewers.

**REFERENCES**


