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Training camp—A way to improve survival in European lobster juveniles?



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ABSTRACT

A series of experiments was conducted to test if keeping hatchery-produced European lobster juveniles (*Homarus gammarus*) in an enriched environment with substrate and shelter would improve anti-predator behaviour and survival in a competition setting. Newly hatched postlarvae (stage IV) were divided into two treatments. Naïve postlarvae were raised in single compartments, while trained postlarvae were released communally into tanks with substrate and shelter, allowing for developing burrowing and shelter-seeking behaviour and interactions with conspecifics. The duration of the treatment lasted 181 days in 2007/2008 and 226 days in 2008/2009. In the second experiment, 4-mo old juveniles were purchased from a commercial hatchery and divided into the same two treatment groups. The treatments were considerably shorter, lasting 47 days. At the end of the treatment period an equal number of juveniles from each treatment was released into experimental units with substrate and shelter i.e. semi-natural system for a period of 91–145 days. Number of shelters was half the total number of juveniles to induce competition for shelters. In both experiments, trained juveniles occupied more shelters and had higher survival than naïve juveniles. Combining all experiments, average survival was 53% in trained lobsters compared with 18% in the naïve lobsters. These results are the first to demonstrate that enriching the hatchery environment for a period of time (a minimum of 47 days here) while rearing European lobster juveniles increased their shelter occupancy and their survival compared to naïve juveniles the same size and age. Survival rates were 3–4 times higher in trained compared to naïve lobsters after 145 days.

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1. Introduction

Efforts to increase recruitment to the fisheries by releasing hatchery-produced juvenile fish or invertebrates have been made for more than 150 years (Munro and Bell, 1997; Nicosia and Lavalli, 1999; Bell et al., 2005). Japan and China have the longest experience, and have to a certain degree also documented success (Uki, 2006; Hamasaki and Kitada, 2006; Wang et al., 2006). In northern Europe, several release programs have focused on the European lobster (*Homarus gammarus*) (Latrouite and Lorec, 1991; Addison and Bannister, 1994; Cook 1995; Agnalt et al., 2004; Schmalenbach et al., 2011). In Norway, hatchery-produced lobster juveniles released over a period of 5 years and monitoring the fishery for 10 years resulted in an overall recapture of 6.2%, ranging from 3.6 to 9.1%, for the various year classes (Agnalt et al., 2004). This is rather high compared with many other release programs,

but Borthen et al. (1999) made an economical analysis on these data and concluded that the recapture rate must be higher than 14% to break-even. This is also in accordance with economic estimates by Moksness et al. (1998).

A major limitation in the Norwegian release experiment was predation immediately after release (van der Meeren, 2000), as also reported in other release programs (e.g. Castro et al., 2001; Daly et al., 2013). In the production of lobster for release purposes, the juveniles are reared individually from the time of settling; i.e. stage IV/postlarvae in plastic boxes with perforated floor (Grimsen et al., 1987). These boxes are bare, except for shell parts or coarse-grained sand in stage V–VII to induce claw development (Govind and Pearce, 1989; Korsøen, 1994). The rearing method provides very few environmental stimuluses, and if and how this affects behaviour is still unknown. Rearing lobster communally, i.e. in open tanks in relatively high numbers with a surplus of food and shelter, offers a more complex set of stimuli. A range of bottom substrates have been tested, from cobble of different sizes to oyster shells and PVC tubes (van Olst et al., 1975; Linnane et al., 2000; Jørstad et al., 2001). The most common method is to use one type of substrate,

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while Jørstad et al. (2001) tested a combination of shell sand supplied with a variety of shelters. Stage IV (postlarvae) released into such complex environment reached sizes comparable to individual rearing and with survival rates of 30–60%, after 4–5 months.

Enhancing behaviour skills like shelter seeking and occupancy as well as social interactions in lobster has not yet been fully explored. Berril (1974) found that burrowing behaviour was based on instincts in newly-settled European lobster. Wickins and Barry (1996) found some evidence of learning or behavioural adaptation. More experiments are needed to look specifically at the physical environment in the hatchery, combined with shelter and predator/prey training (Brown and Day, 2002; Svåsand, 2004; Huntingford, 2004). In this study, we aimed to assess if exposure to substrate and shelter, as well as conspecifics, in the nursery phase can enhance the performance of European lobster juveniles ready-to-be released. We predicted that a training period would enhance shelter occupancy, as well as increase survival compared to naïve juveniles.

2. Material and methods

2.1. Training from postlarvae

2.1.1. Production of postlarvae

The experiment took place at the Institute of Marine Research (IMR) field station at Parisvatnet, Øygarden, located outside Bergen (60°37'N, 4°48'E). Ovigerous females were kept in units (70 × 40 × 25 cm) until hatching. Newly hatched larvae were collected every morning, counted and transferred to 401 upstream incubators (plankton Kreisler, Hughes et al., 1974). The incubators were supplied with aerated sea water at 18–19 °C, 101 min⁻¹. The larvae were fed daily with frozen *Artemia* sp. and frozen krill (*Euphausiidae* sp.). Maximum density for each incubator was set to 50 larvae l⁻¹. The larvae were staged I–IV, according to Sars (1875). The larval stages I–IV are pelagic, but towards the end of stage IV, the postlarvae larvae will settle, and in the wild find suitable substrate for settling. The larvae reached stage IV after 12–14 days.

2.1.2. Treatment

Postlarvae were separated into two treatment groups. One treatment group was raised individually in single-compartments (Fig. 1a); naïve I. The other treatment group was released into tanks (2 × 2 m) where the bottom was covered with 2–3 cm shell sand and shelters (empty valves of scallop) (Fig. 1b); trained. We defined this as enriched environment. The tanks were supplied with filtered ambient sea water. The water depth in the tanks was approximately one meter. It took a few days after the treatment started before the postlarvae settled in the single compartments and in the tanks. The juveniles were fed frozen krill *Euphausia* spp. The first treatment period started 1.7.2007 and ended 11.2.2008 (226 days) and the second treatment period started 11.8.2008 and ended 7.2.2009 (181 days). At the end of the treatment period, carapace length (CL), measured from the anterior part of the orbit to the posterior part of the carapace, was recorded in all juveniles to closest 0.1 mm below with a calliper. Lobster from the two treatment groups were tagged with visible implant elastomer tags (VIE; Northwest Marine Technology Inc) of different colours. The individuals were kept in single-compartment cells for 1–7 days to check for mortality due to the tagging. No mortality was observed. The temperature during the first treatment period was 13.5 ± 1.5 °C during the first 30 days, thereafter slowly decreasing to 5–6 °C at day 140 and was stable at that temperature towards the end. In the second treatment, average temperature the first 30 days was 16.2 ± 0.5 °C, slowly decreased to 8 °C at day 100 and decreased further to 5 °C, and remained such towards the end.

2.1.3. Test arena

Sheltering was defined as an anti-predator mechanism, hence we chose to let the juveniles compete for shelter in a competition arena. We set up four trials, 1–4. Trial 1–2 after the first treatment period and trial 3–4 after the second. In all trials, the juveniles were released into tanks (2 × 2 m; similar to what was used during training treatment and supplied ambient water), bottom covered with 2–3 cm shell sand and shelters (empty valves of scallop). The juveniles were fed frozen krill *Euphausia* spp in excess. In trial 1–2, 20 juveniles of each treatment group (n = 40) were released with 20 shelters. The experiment started 15.2.2008 and ended 15.5.2008 (91 days). In trial 3–4, 40 juveniles of each treatment group were released (n = 80), competing for 40 shelters. These experiments started 11.2.2009 and ended 18.6.2009 (128 days). At the start of the trials, there were no significant differences in carapace length between the treatment groups in trial 1–2 (ANOVA, p > 0.05) and trial 3–4 (ANOVA, p > 0.05). Number of juveniles of each treatment group (naïve and trained) that were found outside shelter, and burrowing activity (seen as piles of sand at the entrances to the shelter) were recorded regularly. At the end of the trials, the number of juveniles of each treatment group outside and within shelter was recorded. One juvenile in trial 1–2 and one in trial 3–4 had lost their elastomer tag at the end of experiment. These two could not be allocated to either treatment and were omitted from further analysis.

2.2. Short-term training of juveniles

2.2.1. Treatment

900 ready-to-be-released juveniles were purchased from Norwegian Lobster Farm AS (NLF) at Kvitsøy, Rogaland (59°24'09"N 05°24'09"E) (www.norwegian-lobster-farm.com). The juveniles were approximately four months old, mean CL = 8.93 ± 0.87 mm, n = 155. They were hatched and on-grown at 19–21 °C, in single-celled compartments deprived of stimuli as substrate and shelter. The juveniles were divided into two treatment groups, naïve and trained. About half of the naïve juveniles were kept in single compartments similar to experiments described in Section 2.1, at ambient temperature of 12 °C (naïve I). The other group was kept in their original single compartments, at temperature 19–21 °C (naïve II). The training treatment was made at the site of NLF in eight flow-through tanks (1 × 1 m), with ambient water temperature at about 12 °C. The bottom of the tanks was covered with 2–3 cm shell sand. 56 juveniles were released into each tank, with 56 shelters available (empty valves of scallop and oyster). The juveniles were fed dry pellets patented by NLF, twice a week. The training started 8.10.2009 and ended 23.11.2009 (47 days).

2.2.2. Test arena

For this experiment we decided to move from a tank-system to a semi-natural system in a lobster holding park facility at Kvitsøy, in the vicinity of NLF. Historically, the park was a holding facility for commercially captured lobster, a rectangular building partly submerged in the intertidal zone with water exchange at each short side. Two meshed netting enclosures of 12 m² (3 × 4 m) were placed at 2.0–2.5 m depth in the lobster park (Trial 5–6). The netting reached above the water surface and was attached with ropes to the park ceiling. 26 scallop baskets (60 × 60 cm) were set on the bottom of the enclosures, with 2–3 cm shell sand (Boston AS). In each enclosure, 260 shelters (empty valves of great scallop and oyster) were added. The enclosures were set up on 8 October 2009 allowing the system to be established before the experiment started.

In preparation for the experiment, we noted that the juveniles in the naïve II treatment were in general in a poorer condition than naïve I. We decided to treat the two naïve groups as two separate treatments. Naïve II was given two days to acclimatize to the same

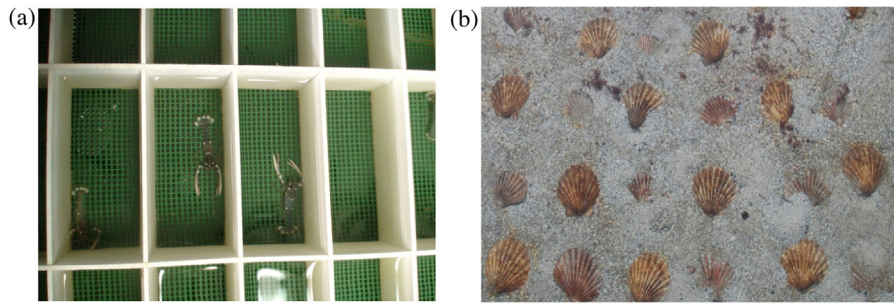


Fig. 1. The two treatments used in the training experiments (a) naïve lobster juveniles raised in single-cell compartments (naïve I) and (b) trained juveniles raised in a more complex environment with shell sand, shelter and interaction with conspecifics.

temperature as provided for naïve I and trained juveniles. In the training treatment, we noticed there were juveniles outside the shelters, and decided to tag these as a separate group (vagrant). Lobsters from the different treatment groups were tagged with VIE tags of different colours. Mean CL (mm) naïve I = 10.1 ± 0.9 ; naïve II = 10.3 ± 0.7 ; trained = 10.4 ± 1.0 ; vagrant = 11.4 ± 1.0 . There were no significant differences in size (ANOVA, $p=0.87$). We aimed to release equal numbers of juveniles in each trial, but when summing up the numbers, a total of 454 juveniles was released in trial 5 and 395 in trial 6. In trial 5, we used 125 naïve I, 125 naïve II, 162 trained and 42 vagrant juveniles, and in trial 6, 72 naïve I, 122 naïve II, 162 trained and 39 vagrant juveniles. The competition experiment started 23.11.2009 and ended 16.4.2010 (145 days). Feed was given as fish offal three times during the experiment, approximately once every six to seven weeks. At the end of the experiment, number of juveniles from each treatment was counted and CL was recorded. None of the surviving juveniles had lost their elastomer tag during

this period. For statistical analysis, CL was compared between treatments and trials with ANOVA. For comparing separate treatments, a simple student *t*-test, two-sample assuming unequal variance was used.

2.3. Descending speed and behaviour

Juveniles from each treatment were released at the surface and the time in seconds it took to reach the tank bottom was recorded. The depth of the water tank varied from 26 to 38 cm, and the descending speed is given as seconds per cm. The descending speed was recorded before releasing the juveniles into the competition experiments in trial 1–6. We decided to record descending speed also at the end of the competition experiment to analyze possible changes. This was done in the experiment with short-term training of commercially produced juveniles, and where the test arena was a semi-natural system (trial 5–6). Non-parametric

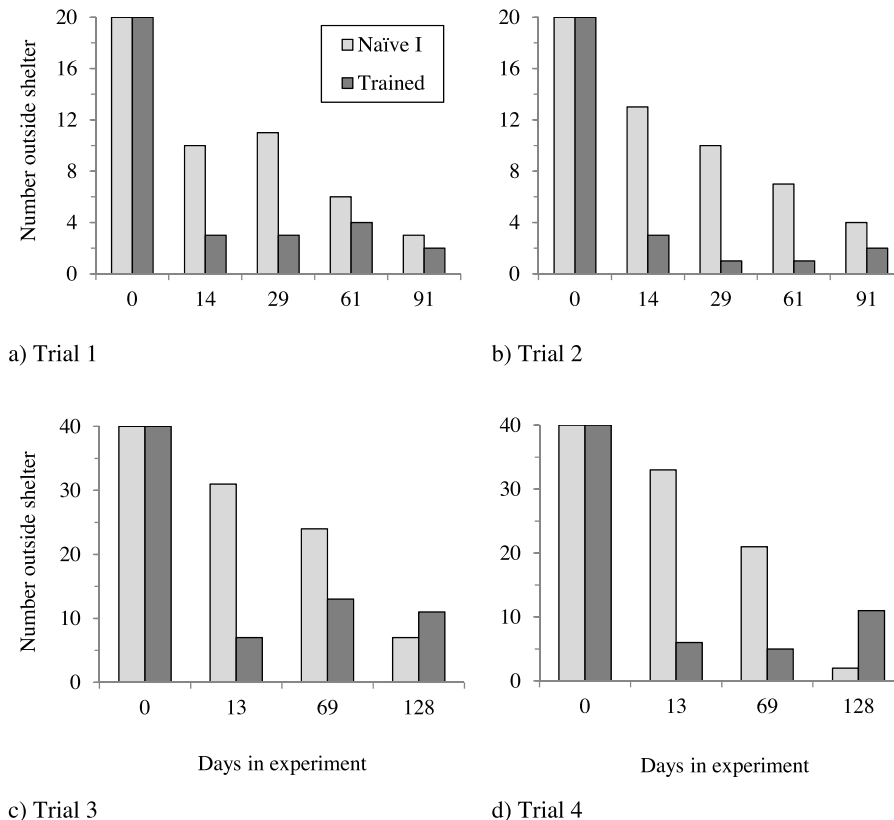


Fig. 2. Number of naïve and trained lobster juveniles found outside shelter in the competition experiment. Number of shelters was half of the total number of juveniles released in each trial. Trial 1–2 was conducted in 2008, and trial 3–4 in 2009.

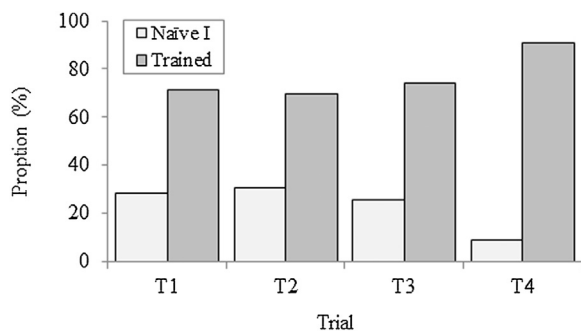


Fig. 3. Proportion surviving lobster juveniles from naïve I and trained treatment in trial 1–4 at the end of the competition experiment.

Kolmogorov-Smirnov was used to test differences in descending speed comparing treatments and trials. Descending behaviour was quantified in trial 5–6 as sinking passively without any movement of appendages or body to the bottom (1); floating, usually spreading the claws like an umbrella, backwards as well as forwards (2); swimming, forward or backwards with or without spreading of claws (3); torpedo, swimming fast with claws closed forward in front of the head and moving actively towards the bottom with head first (4). Descending behaviour was recorded for 42 naïve I, 83 naïve II, 42 trained and 41 vagrant juveniles.

3. Results

3.1. Training from stage IV larvae

In overall, more naïve than trained juveniles were found outside shelter (Fig. 2). The only exception was at the end the experiment in trial 3–4, but was probably due to increased temperatures and overall increased activity. The majority of those found outside shelter had lost one or both claws. 14 days after release, about half (50 and 55%) of the initially released naïve juveniles in trial 1–2 were found outside shelter, compared with 5 and 15% of the trained juveniles. In trial 3–4, as much as 85 and 83%, respectively, of the initially released naïve juveniles were found outside shelter at day 14, compared with 17 and 15% of the trained juveniles. Burrowing activity was observed on average at around 91% of the shelters in all trials combined at day 14. At the end of the experiment, 50 and 80% of the shelters were occupied in trial 1–2, and 48 and 71% in trial 3–4. Naïve juveniles constituted from 9 to 30% of the total number of surviving lobster juveniles (Fig. 3). Of these, 48–71% were found within shelter. On average, 88% of those juveniles within shelters were trained. Total survival ranged from 7.5 to 35% in naïve compared with 50 to 80% in the trained juveniles. The mean size of the surviving naïve and trained juveniles was similar in trial 1–2, as also observed in trial 3–4 (Table 1). There was a tendency for juveniles found inside shelter to be larger compared with those found outside shelter, but this was not statistically testable due to low numbers in the naïve treatment.

3.2. Short-term training of juveniles

Total survival in trials 5 and 6 was 19.6% and 7.1%, respectively (see Table 1 for numbers). The difference could be related to the positioning of the enclosures, as trial 5 was closest to the water inlet thus providing higher quality water regarding e.g. oxygen levels. Total survival of each treatment was 18% in naïve I, 2% in naïve II, 44% in trained and 25% in vagrant juveniles. Of the surviving juveniles, trained comprised 71% compared with 18% naïve I (Fig. 4). At the end of the competition experiment, trained juveniles were in

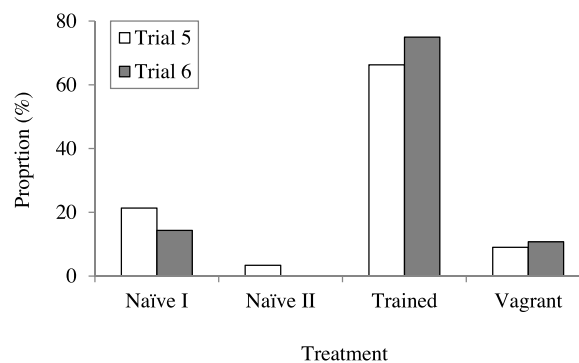


Fig. 4. The proportion of surviving lobster juveniles in each treatment naïve I, naïve II, trained and vagrant in trial 5 and 6.

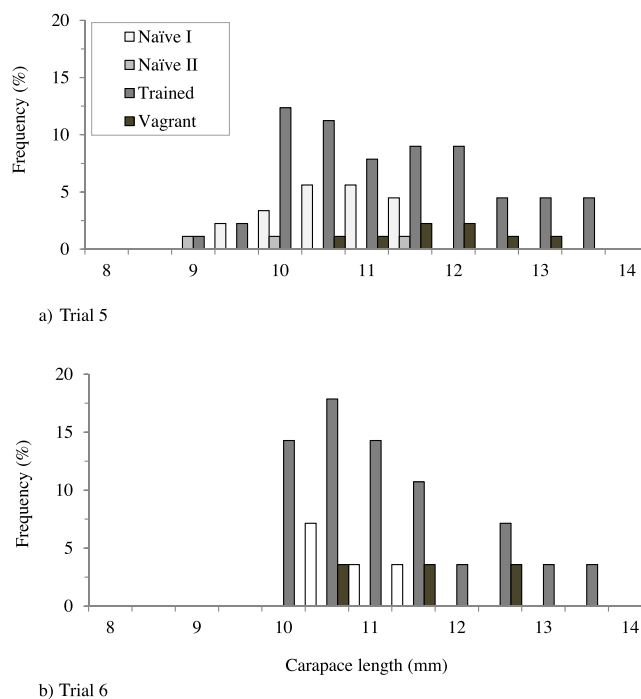


Fig. 5. Frequency of carapace length distribution in the surviving lobster juveniles after 145 days in a semi-natural system with no predators present except conspecifics, for the different treatments, naïve I, naïve II, trained and vagrant in (a) trial 5 and (b) trial 6.

general found over a larger size range than naïve juveniles (Fig. 5, Table 1). Due to low survival numbers in trial 6, only trial 5 was tested. Naïve I were significantly smaller than trained juveniles and vagrant (*t*-test; one-tail, $p < 0.05$). There were no significant differences between trained and vagrant (*t*-test, $p = 0.17$).

Table 1

Mean carapace length (CL) (mm) with standard deviation and number of juveniles from each treatment that survived during the competition experiments in trial 1–6.

Trial	Naïve I	Naïve II	Trained	Vagrant
1	9.9 ± 1.1 (n = 19)	–	10.2 ± 1.5 (n = 18)	–
2	9.6 ± 0.9 (n = 27)	–	9.9 ± 1.5 (n = 20)	–
3	12.4 ± 1.2 (n = 9)	–	11.9 ± 1.7 (n = 26)	–
4	11.2 ± 0.6 (n = 3)	–	12.7 ± 1.8 (n = 30)	–
5	10.9 ± 0.6 (n = 19)	10.4 ± 1.3 (n = 3)	11.5 ± 1.1 (n = 59)	12.0 ± 0.8 (n = 8)
6	11.2 ± 0.3 (n = 4)	no survivors	11.4 ± 1.1 (n = 21)	11.7 ± 0.4 (n = 3)

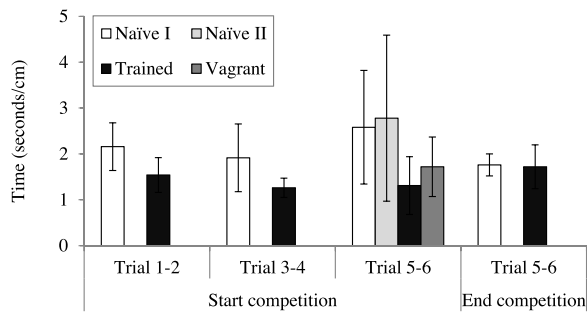


Fig. 6. Descending speed ($s\text{ cm}^{-1}$) from release at surface to reaching the bottom for treatments naïve I, naïve II, trained and vagrant in trial 1–6.

Table 2

Number of lobster juveniles from each treatment naïve I, naïve II, trained and vagrant in trial 5–6 that descended from surface to bottom of the tank either/or Sinking, Floating, Swimming or Torpedo or a combination (Combo). The observations were made at the start of the competition experiment and repeated at the end.

Behaviour category	Start				End	
	Naïve I	Naïve II	Trained	Vagrant	Naïve I	Trained
Sinking	1	10	5	10	19	5
Floating	2	4	27	3	3	11
Swimming	3	11	18	10	4	6
Torpedo	4		1	3	3	1
Combo	1+2	3	2	2	3	3
	1+3	10	2	11	6	
	1+4		0			
	2+3	2	23	1		
	2+4		1			
	3+2			1		
	3+4	1	1	5	2	
	1+2+3	1	4	2	1	
	1+3+4			2		
Total N	42	83	42	41	19	20

3.3. Descending speed and behaviour

When starting the competition experiment, naïve juveniles in trial 1–4 descended at an average speed of 2.0 s cm^{-1} , compared with trained juveniles, which used less time, 1.4 s cm^{-1} (Fig. 6). The difference was significant in trial 1–2 ($p < 0.01$; Kolmogorov-Smirnov) and in trial 3–4 ($p < 0.01$). In trial 5–6, the average descending speed was similar in naïve I and II at the start of the competition experiment ($p > 0.01$), averaging 2.7 s cm^{-1} . There was a significant difference in descending speed comparing naïve I with trained ($p < 0.01$), and trained differed from vagrant ($p < 0.01$). Trained juveniles spent 1.3 s cm^{-1} and vagrant juveniles 1.7 s cm^{-1} . At the end of the competition experiment, the descending speed was not significantly different comparing naïve and trained juveniles ($p > 0.01$), 1.8 and 1.7 s cm^{-1} respectively.

When starting the competition experiment, trial 5–6, 50–70% of the juveniles performed one descending behaviour while the remaining made a combination of several behaviours (Table 2). The naïve I juveniles were sinking and/or swimming (74%), naïve II were floating and/or swimming (82%), trained juveniles were floating and/or swimming (74%) while 46% of vagrants were floating (Table 2). Only a few juveniles used the torpedo behaviour (7%), often in combination with other descending behaviour. However, of those that used torpedo, 81% were trained, including the vagrant. At the end of the competition experiment, the descending behaviour had changed some, as floating was the dominant descending behaviour among naïve I juveniles (58%) and trained (65%).

4. Discussion

This is the first study to show that enriching the environment of hatchery-reared European lobster juveniles increased their shelter occupancy and increased their survival in the hatchery when competing with naïve juveniles the same size and age. Training from the settling stage IV and for a minimum of 181 days gave similar results as training juveniles for a shorter period, 47 days.

The environment in a hatchery is very different from what the animals will experience in the wild, providing protection in a range of parameters, such as stable temperature and salinity, absence of predators, excess of feed (artificial) and medication in case of a disease outbreak. This may seem beneficial, but hatchery-induced changes have been described in a number of species (Olla et al., 1998; Svåsand et al., 1998; Tsukamoto et al., 1999) and a number of papers have addressed this problem along with recommendations to improve rearing conditions (Huntingford, 2004; Brown et al., 2003; Salvanes and Braithwaite, 2006). Some changes in shellfish are morphological, such as lower shell strength in great scallop (*Pecten maximus*) and queen conch (*Strombus gigas*), lack of spikes in topshell (*Trochus niloticus*), or lack of differentiation in the claws in lobster (*Homarus* spp) (Govind and Pearce, 1989; Stoner and Davis, 1994; Purcell, 2002; Grefsrud and Strand, 2006; Agnalt, 2008). In our experiments, we used shell sand and shelters to promote burrowing and shelter-related behaviour, and kept juveniles in large groups, promoting social interactions. Thus rearing juveniles on natural substrate is likely to improve post-release survival. However, the mechanism for the improvement is not clear. Did exposure to shell sand elicit the difference or was it shelter occupancy alone or in combination, or was it interactions with conspecifics? We do not know, and each of these stimuli should be tested in future experiments. Aspaas et al. (2016) studied shelter behaviour in hatchery-produced lobster juveniles, but could not identify behavioural changes resulting from training. European lobster juveniles less than 20 mm carapace length have never been found in the wild (Linnane et al., 2001; Mercer et al., 2001), so natural or even unnatural behaviour is unknown. In the wild, there are also other predators present and if and how the juveniles respond is something that should be explored further. More studies are therefore needed to identify the mechanisms to better understand processes to be implemented in the training phase.

van der Meeren (2001) found indications that previous sheltering experience in European lobster juveniles was an advantage in a new environment, as experienced juveniles used less time in finding and accepting shelter compared with naïve juveniles. The ability to learn might be linked to a specific window of time during ontogenic development. The early-benthic phase of European lobster is typically cryptic, but later behaviour changes, resulting in either a habitat switch or increased movement range (Linnane et al., 2001; Mercer et al., 2001). In our experiments, training postlarvae for four months or training hatchery-produced juveniles for seven weeks yielded comparable survival, indicating that learning capacity in the early life stages is extensive. Learning is closely linked with memory, and in crayfish (*Cherax destructor*) the production of neurons in the part of the brain associated with the olfactory, visual and tactile receptor system increased in communally-held individuals given space and social interactions as stimuli, compared with those kept in single compartments (Sandeman and Sandeman, 2000).

The ability to remember conspecifics and predators has been shown for a variety of species, including American lobsters (Utne-Palm, 2001; Kelley and Magurran, 2003; Johnson and Atema, 2005; Gherardi et al., 2010). Lobsters use urine pheromones via chemoreceptors for individual recognition and have a memory of previous interactions (Karavanich and Atema, 1998; Johnson and Atema, 2005; Skog, 2008). They remember the outcome of previous fights, and a loser will avoid new interactions with a previous winner.

Memory has been shown to last from one to two weeks. In our experiments, the trained juveniles were kept in single compartments for up to seven days before released and could potentially still have a memory of the hierarchical dominance structure. When entering into a new environment with new competitors, the juveniles at the bottom of the hierarchy may be more cautious and lose when competing for a shelter. This could possibly explain the poor survival of vagrant juveniles in trial 5–6. Future experiments should tag the different groups of juveniles, those within and outside shelter to evaluate this hypothesis. The low survival in naïve juveniles may reflect the lack of previous social interactions, as van der Meeren (1993) and Aspaas et al. (2016) have shown that naïve juveniles are more aggressive and involved in more fights compared with trained juveniles, thus spending less time finding and defending shelter.

In lobster, sheltering is an important anti-predator response (van der Meeren, 1993). In the presence of cunner (*Tautoglabrus adspersus*), wild American lobster postlarvae spent all their time within shelter compared with 40–80% in hatchery-reared naïve postlarvae (Castro and Cobb, 2005). Predation has been shown to be significant in a release situation (Barshaw and Lavalli, 1988; van der Meeren, 2000; Oliver et al., 2010; Daly et al., 2013; Johnson et al., 2008). Predation was highest about 2 h after releasing rock lobster (*Jasus edwardsii*) (Oliver et al., 2010), and in European lobster, 10% were consumed by various fish species within the first hour (van der Meeren, 2000). We found that training European lobster juveniles resulted in increased shelter occupancy and survival, compared with naïve juveniles. Trained juveniles outnumbered naïve ones three to four times. We believe the complexity in the training environment improved their ability to survive. However, field experiments are needed to verify the findings from laboratory and semi-natural systems. For instance, predator training of Atlantic cod juveniles in laboratories was successful, but did not cause higher survival rates when released into the wild (Otterå et al., 1999). Whether training juveniles affords an advantage in a release situation with other predators present needs to be further addressed (e.g. Oliver et al., 2006, 2008).

European lobster juveniles smaller than 40 mm CL have rarely been captured in the wild (Linnane et al., 2001; Mercer et al., 2001). In contrast, young-of-the-year of their relative, the American lobster, are found in a variety of substrates (Wahle et al., 2013). Despite intensive searching in areas/countries with high landings of legal-sized European lobster, habitat preference of small juveniles is still unknown. This makes it difficult to design release methods based on habitat and shelter preferences. Progress would be advanced in commercial restocking or sea ranching projects by being able to select juveniles that have increased probability of surviving. We looked at descending speed and behaviour, and although trained juveniles were faster than naïve juveniles in our study, this needs to be further elaborated. Training to recognize specific substrates might also overcome high predation pressure immediately after release. Future studies should also address if lobster juveniles are able to identify odor from potential predators like wrasses or crabs.

5. Conclusion

Our results demonstrate that experience of environmental complexity and social interactions increases shelter-seeking ability and survival in hatchery reared European lobster juveniles. Trained juveniles occupied more shelters, had reduced descending speed and higher survival compared with naïve juveniles. In the large-scale release at Kvitsøy, Agnalt et al. (2004) found an overall recapture rate of 10% when releasing naïve hatchery-reared lobster juveniles. To make lobster sea ranching a viable industry in Norway, recapture rate needs to be at least 15%. Our study shows

that implementing a training period increased survival in a competition setting by threefold. Although the juveniles in the present study were not exposed to known predators, such as cod, wrasse or shore crabs, a behaviour that reduces time spent in the water column and shelter seeking time should be a clear advantage in a release situation. A large-scale field experiment is needed to confirm if training provides the same advantage in the wild that we found in our study in the laboratory.

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References

- Addison, J.T., Bannister, R.C.A., 1994. Re-stocking and enhancement of clawed lobster stocks: a review. *Crustaceana* 67, 131–155.
- Agnalt, A.-L., Jørstad, K.E., Kristiansen, T., Nøstvold, E., Farestveit, E., Næss, H., Paulsen, O.I., Svåsand, T., 2004. Enhancing the European lobster (*Homarus gammarus*) stock at Kvitsøy Islands; Perspectives of rebuilding Norwegian stocks, p. 415–426. In: Leber, K.M., Kitada, S., Blankenship, H.L., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching. Developments, Pitfalls and Opportunities*. Blackwell Publishing Ltd, Oxford, p. 562.
- Agnalt, A.-L., 2008. Stock enhancement of European lobster (*Homarus gammarus*) in Norway; Comparisons of reproduction, growth and movement between wild and cultured lobster. In: Dr. Scient. Thesis. Department of Biology, University of Bergen, Norway, pp. 56.
- Aspaas, S., Grefsrud, E.S., Fernö, A., Jensen, K.H., Trengereid, H., 2016. An enriched environment promotes shelter-seeking behaviour and survival of hatchery-produced juvenile European lobster (*Homarus gammarus*). *PLoS ONE* 11 (8), <http://dx.doi.org/10.1371/journal.pone.0159807>, e0159807.
- Barshaw, D.E., Lavalli, K.L., 1988. Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautoglabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, bud and rocks. *Mar. Ecol. Prog. Ser.* 48, 119–123.
- Bell, J.D., Rothlisberg, P.C., Munro, J.L., Loneragan, N.R., Nash, W.J., Ward, R.D., Andrew, N.L., 2005. Restocking and stock enhancement of marine invertebrates fisheries. *Adv. Mar. Biol.* 49, 374.
- Berril, M., 1974. The burrowing behaviour of newly-settled lobsters *Homarus vulgaris* (Crustacea-Decapoda). *J. Mar. Biol. Assoc. U. K.* 54, 797–801.
- Borthen, J., Agnalt, A.-L., van der Meeren, G.I., 1999. A bio-economical evaluation of a stock-enhancement project of European lobster; The simulation model LOBST.ECO with some preliminary results, p. 583–596. In: Howell, B., Moksness, E., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books, Blackwell Science, Oxford, p. 606.
- Brown, C., Day, R.L., 2002. The future of stock enhancements: lessons for hatchery practise from conservation biology. *Fish Fish.* 3, 79–94.
- Brown, C., Davidson, T., Laland, K., 2003. Environmental enrichment and prior experience of live prey improve foraging behaviour in hatchery-reared Atlantic salmon. *J. Fish Biol.* 63 (Suppl. A), 187–196.
- Castro, K.M., Cobb, J.S., 2005. Behaviour of hatchery -reared and wild-caught 4th and 5th stage American lobsters, *Homarus americanus*. *N. Z. J. Mar. Freshw. Res.* 39, 963–972.
- Castro, K.M., Cobb, J.S., Wahle, R.A., Catena, J., 2001. Habitat addition and stock enhancement for American lobsters, *Homarus americanus*. *Mar. Freshw. Res.* 52, 1253–1261.
- Cook, W., 1995. *A Lobster Stock Enhancement Experiment in Cardigan Bay, Final Report*. North Western and North Wales Fisheries Committee, University of Lancaster 33.
- Daly, J., Eckert, G.L., White, T.D., 2013. Predation of hatchery-cultured juvenile red king crabs (*Paralithodes camtschaticus*) in the wild. *Can. J. Fish. Aquat. Sci.* 70, 358–366.
- Gherardi, F., Cenni, F., Parisi, G., Aquiloni, L., 2010. Visual recognition of conspecifics in the American lobster, *Homarus americanus*. *Anim. Behav.* 80, 713–719.
- Govind, C.K., Pearce, J., 1989. Critical period for determining claw asymmetry in juvenile lobsters. *J. Exp. Zool.* 249, 31–35.

- Grefsrud, E.S., Strand, Ø., 2006. Comparison of shell strength in wild and cultured scallops (*Pecten maximus*). *Aquaculture* 251, 306–313.
- Grimsen, S., Jaques, R.N., Erenst, V., Balchen, J.G., 1987. Aspects of automation in a lobster farming plant. *Model. Identif. Control* 8, 61–68.
- Hamasaki, K., Kitada, S., 2006. A review of kuruma prawn *Penaeus japonicus* stock enhancement in Japan. *Fish. Res.* 80, 80–90.
- Hughes, J.T., Shleser, R.A., Tchobanoglous, G., 1974. A rearing tank for lobster larvae and other aquatic species. *Progress. Fish Cult.* 36, 129–132.
- Huntingford, F.A., 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J. Fish Biol.* 65 (Suppl. A), 122–142.
- Jørstad, K.E., Nøstvold, E., Kristiansen, T.S., Agnalt, A.-L., 2001. High survival and growth of European lobster juveniles (*Homarus gammarus*): reared communally with natural bottom substrate. *Mar. Freshw. Res.* 52, 1431–1438.
- Johnson, M.E., Atema, J., 2005. The olfactory pathway for individual recognition in the American lobster *Homarus americanus*. *J. Exp. Biol.* 208, 2865–2872.
- Johnson, E., Hines, A.H., Kramer, M.A., Young, A.C., 2008. Importance of season and size of release to stocking success for the blue crab in Chesapeake Bay. *Rev. Fish. Sci.* 16, 243–253.
- Karavanich, C., Atema, J., 1998. Individual recognition and memory in lobster dominance. *Anim. Behav.* 56, 1552–1560.
- Kelley, J., Magurran, A.E., 2003. Learned predator recognition and antipredator responses in fishes. *Fish. Sci.* 4, 216–226.
- Korsøen, E., 1994. Survival, growth and claw morphology, related to numbers of scissor claws at metamorphosis, and the bottom substrate in juvenile lobster *Homarus gammarus*. In: Master Thesis. University of Bergen, Norway, pp. 65 (in Norwegian).
- Latrouite, D., Lorec, J., 1991. L'expérience française de forçage du recrutement du homard européen (*Homarus gammarus*): resultants préliminaires. *ICES Mar. Sci. Symp.* 192, 93–98.
- Linnane, A., Ball, B., Munday, B., Mercer, J.P., 2000. A long-term mesocosm study on the settlement and survival of juvenile European lobster *Homarus gammarus* L. in four natural substrata. *J. Exp. Mar. Biol. Ecol.* 249, 51–64.
- Linnane, A., Ball, B., Mercer, J.P., Browne, R., van der Meer, G.I., Ringvold, H., Bannister, R.C.A., Mazzoni, D., Munday, B.W., 2001. Searching for the early benthic phase (EBP) of the European lobster: a trans-European study of cobble fauna. *Hydrobiologia* 465, 63–72.
- Mercer, J.P., Bannister, R.C.A., van der Meer, G.I., Debuse, V., Mazzoni, D., Lovewell, S., Browne, R., Linnane, A., Ball, B., 2001. An overview of the LEAR (Lobster Ecology and Recruitment) project: results of field and experimental studies on the juvenile ecology of *Homarus gammarus* in cobble. *Mar. Freshw. Res.* 52, 1291–1301.
- Moksness, E., Støle, R., van der Meer, G., 1998. Profitability analysis of sea ranching with Atlantic salmon (*Salmo salar*), arctic charr (*Salvelinus alpinus*), and European lobster (*Homarus gammarus*) in Norway. *Bull. Mar. Sci.* 62 (2), 689–699.
- Munro, J.L., Bell, J.D., 1997. Enhancement of marine fisheries resources. *Rev. Fish. Sci.* 5, 185–222.
- Nicosia, F., Lavalli, K., 1999. Homarid lobster hatcheries: their history and role in research, management and aquaculture. *Mar. Fish. Rev.* 61, 1–57.
- Oliver, M.D., MacDiarmid, A.B., Stewart, R., Gardner, C., 2006. Spiny lobster population enhancement: moderation of emergence behaviour of juvenile *Jasus edwardsii* reared in captivity. *N. Z. J. Mar. Freshw. Res.* 40, 605–613.
- Oliver, M.D., MacDiarmid, A.B., Stewart, R., Gardner, C., 2008. Anti-predator behavior of captive-reared and wild juvenile spiny lobster (*Jasus edwardsii*). *Rev. Fish. Sci.* 16, 186–194.
- Oliver, M.D., Stewart, R., Mills, D., Macdiarmid, A.B., Gardner, C., 2010. Stock enhancement of rock lobsters (*Jasus edwardsii*): timing of predation on naïve juvenile lobsters immediately after release. *N. Z. J. Mar. Freshw. Res.* 39, 391–397.
- Olla, B.L., Davis, M.W., Ryer, C.H., 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bull. Mar. Sci.* 62, 531–550.
- Otterå, H., Kristiansen, T.S., Svåsand, T., Nødtvedt, M., Borge, A., 1999. Sea-ranching of Atlantic cod (*Gadus morhua* L.): effects of release strategy on survival. In: Howell, B., Moksness, E., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books, Blackwell Science Ltd, Oxford, p. 606.
- Purcell, S., 2002. Cultured vs wild juvenile trochus: disparate shell morphologies send caution for seeding. *SPC Trochus Inf. Bull.* 9, 6–8.
- Salvanes, A.G.V., Braithwaite, V., 2006. The need to understand the behaviour of fish reared for mariculture or restocking. *ICES J. Mar. Sci.* 63, 346–354.
- Sandeman, R., Sandeman, D., 2000. Improperly reared and Enriched living conditions influence the proliferation and survival of neurons in crayfish brain. *J. Neurobiol.* 45, 215–226.
- Sars, G.O., 1875. Om hummerens postembryonale udvikling (About the lobsters post-embryo development). Christiania Videnskabs-Selskabs Forhandling, Brøgers Boktrykkeri. Christiania, 1–27, +2 plates.
- Schmalenbach, I., Mehrtens, F., Janke, M., Buchholz, F., 2011. A mark-recapture study of hatchery-reared juvenile European lobsters, *Homarus gammarus*, released at the rocky island of Helgoland (German Bight, North Sea) from 2000 to 2009. *Fish. Res.* 108, 22–30.
- Skog, M., 2008. Sex and violence in lobsters – a smelly business. Olfactory-based communication in the European lobster. In: Doctoral Thesis. Lund University, Sweden, pp. 48.
- Stoner, A.W., Davis, M., 1994. Experimental outplanting of juvenile queen conch, *Strombus gigas*: comparison of wild and hatchery-reared stocks. *Fish. Bull.* 92, 390–411.
- Svåsand, T., Skilbri, O.T., van der Meer, G.I., Holm, M., 1998. Review of morphological and behavioural differences between reared and wild individuals: implications for sea-ranching of Atlantic salmon, *Salmo salar* L., Atlantic cod, *Gadus morhua* L., and European lobster, *Homarus gammarus* L. *Fish. Manag. Ecol.* 5, 473–490.
- Svåsand, T., 2004. Why juvenile quality and release strategies are important factors for success in stock enhancement and sea ranching. In: Leber, K.M., Kitada, S., Blankenship, H.L., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching. Developments, Pitfalls and Opportunities*, 562. Blackwell Publishing Ltd, Oxford.
- Tsukamoto, K., Kuwada, H., Uchida, K., Masuda, R., Sakaura, Y., 1999. Fish quality and stocking effectiveness: behavioural approach. In: Howell, B., Moksness, E., Svåsand, T. (Eds.), *Stock Enhancement and Sea Ranching*. Fishing News Books, Blackwell Science Ltd, Oxford, p. 606.
- Uki, N., 2006. Stock enhancement of the Japanese scallop *Patinopecten yessoensis* in Hokkaido. *Fish. Res.* 80, 62–66.
- Utne-Palm, A.C., 2001. Response to naïve two-spotted gobies *Gobiusculus flavescens* to visual and chemical stimuli of their natural predator cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 218, 267–274.
- Wahle, R., Bergeron, C., Tremblay, J., Wilson, C., Burdett-Coutts, V., Comeau, M., Rochette, R., Lawton, P., Glenn, R., Gibson, M., 2013. The geography and bathymetry of American lobster benthic recruitment as measured by diver-based suction sampling and passive collectors. *Mar. Biol. Res.* 9, 42–58.
- Wang, Q., Zhuang, S., Deng, J., Ye, Y., 2006. Stock enhancement and translocation of the shrimp *Penaeus chinensis* in China. *Fish. Res.* 80, 67–79.
- Wickins, J.F., Barry, J., 1996. The effect of previous experience on the motivation to burrow in early benthic phase lobsters (*Homarus gammarus* (L.)). *Mar. Freshw. Behav. Physiol.* 28, 211–228.
- van Olst, J.C., Carlberg, J.M., Ford, R.F., 1975. Effects of substrate type and other factors on growth survival and cannibalism of juvenile, *Homarus americanus*, in mass rearing systems. *Proc. World Maricult. Soc.* 6, 261–274.
- van der Meer, G.I., 1993. Initial response to physical and biological conditions in naïve juvenile lobsters *Homarus gammarus* L. *Mar. Behav. Physiol.* 24, 79–92.
- van der Meer, G.I., 2000. Predation on hatchery-reared lobsters released in the wild. *Can. J. Fish. Aquat. Sci.* 57, 1794–1803.
- van der Meer, G.I., 2001. Effects of experience with shelter in hatchery-reared juveniles European lobster *Homarus gammarus*. *Mar. Freshw. Res.* 52, 1487–1493.