Predation on hatchery-reared lobsters released in the wild

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Abstract: Predation on hatchery-reared lobsters (*Homarus gammarus*) in the wild was studied in order to identify predators in southwestern Norway on rocky and sandy substrates in winter and summer. Lobsters of 12–15 mm carapace length were tagged with magnetic microtags. About 51 000 juvenile lobsters were released on 10 occasions at three locations. Predator samplings were by trammel nets, eel traps, and videorecordings during the 24 h immediately following the releases. In summer, loss to predators occurred on both rocky and sandy substrates. The loss was lower in winter when lobsters were found as prey in predators caught on sand. The risk of fish predation was highest in the first hours after release, when the lobsters were out of shelter. The wrasses *Labrus bergylta* and *Labrus mixtus* were the major predators of lobsters, while Atlantic cod (*Gadus morhua*), shorthorn sculpin (*Myoxocephalus scorpius*), and crab (*Cancer pagurus*) were mainly winter predators. Winter predators were never as abundant as summer predators. To minimise predatory loss of reared and costly lobsters, they should be released onto rocky substratum in winter. Due to the damage to the predated lobsters, it was not possible to correlate survival against lobster size.

Résumé : Nos études, menées dans le sud-ouest de la Norvège sur la prédation exercée dans le milieu naturel sur des homards d'élevage (*Homarus gammarus*), visaient à identifier les prédateurs sur des substrats rocheux et sableux, en hiver et en été. Des homards dont la longueur de carapace était de 12–15 mm ont été étiquetés avec des micromarques magnétiques. Environ 51 000 homards juvéniles ont été lâchés en dix occasions à trois endroits. Pour échantillonner les prédateurs, on a eu recours à des trémails, des pièges à anguille et des enregistrements vidéo pendant les 24 h qui suivaient immédiatement les lâchers. En été, la prédation se produisait à la fois sur les substrats rocheux et sur les substrats sableux. Elle était moins intense en hiver, les prédateurs ayant consommé des homards se retrouvant surtout sur le sable. Le risque de prédation par des poissons était au maximum dans les premières heures qui suivaient le lâcher, lorsque les homards étaient dépourvus d'abris. Les labres *Labrus bergylta* et *Labrus mixtus* étaient les principaux prédateurs des homards, tandis que la morue (*Gadus morhua*), le chaboisseau (*Myoxocephalus scorpius*) et le crabe (*Cancer pagurus*) étaient surtout des prédateurs d'hiver. Les prédateurs d'hiver n'ont jamais été aussi abondants que les prédateurs d'été. Pour minimiser les pertes par prédation des coûteux homards d'élevage, il faudrait les lâcher en hiver sur des substrats rocheux. Étant donné les dommages subis par les homards soumis à la prédation, il n'a pas été possible de corréler la survie à la taille des homards.

[Traduit par la Rédaction]

Introduction

Releases of reared juvenile lobsters (*Homarus* sp.) have been made for more than 100 years on both sides of the North Atlantic Ocean (Addison and Bannister 1994), including Norway (Appelöf 1909; Dannevig 1928; Tveite and Grimsen 1995). Through the development of the magnetic binary-coded microtag, it is possible to tag lobster juveniles before release into the sea for recognition years later in commercial landings (Jefferts et al. 1963; Wickins et al. 1986). A series of releases of tagged juvenile lobsters have since been conducted in Europe (Latrouite and Lorec 1991; Bannister et al. 1994; Agnalt et al. 1999).

In Norway, a large-scale lobster hatchery at Kyrksæterøra was built in 1973 to produce juvenile European lobsters (*Homarus gammarus*) for stock enhancement and commercial sea ranching (Grimsen et al. 1987). Since 1988, the Institute of Marine Research has studied the potential benefit of releasing juveniles into local lobster stocks (Borthen et al. 1998).

Information on predators of juvenile European lobsters is scarce and is usually based on anecdotes and not quantified observations during release of reared juveniles (Howard 1983; van der Meeren 1991). The aim of this paper is to identify seasonal variation in lobster loss to predators in the first 24 h following release, compare lobster loss to predators after release to rocky versus sandy bottom, and identify species of lobster predators and their occurrence and activity as predators during different seasons. Recommendations to reduce loss of juvenile lobsters in future releases will be made.

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Materials and methods

Study sites

The research program, conducted between 1988 and 1994, consisted of two main components. First, there were a series of large-scale releases to evaluate the possibility of enhancing local lobster stocks, and hence the fishery (Agnalt et al. 1999). This project component was undertaken within the context of the Norwegian Sea Ranching Programme (PUSH) and in cooperation with local fishermen. Lobsters were released at the complex archipelago of Kvitsøy, which has approximately 81 700 km of shoreline (Fig. 1). The project's second component was designed to evaluate how, when, and where to release lobster juveniles so as to minimize postrelease loss. These latter releases took place at selected locations at Øygarden and Huftarøy, Hordaland County, Norway (Fig. 1). The releases at Øygarden were conducted in Langøysundet, a narrow sound with shorelines exhibiting well-defined areas of rocky substrate covered with boulders and cobble (rocks) and also areas with soft bottoms (sand). Lobsters were released onto each habitat type. At Huftarøy, lobsters were released by divers onto three rocky areas simultaneously and in patches of high density.

Techniques for low-cost transportation and large-scale (>20 000 individuals·day^{-1}) release of lobster juveniles, as well as lobster behaviour in the first minutes after a release, have been described elsewhere (van der Meeren 1991, 1993).

Tagging and release techniques

Lobsters were hatched and reared at the large-scale lobster hatchery, Kyrksæterøra, Norway. Lobsters released from 1990 to 1994 were tagged with magnetic binary-coded microtags (North West Marine Technology Inc.) at 5–8 months of age, which represented a carapace length of approximately 12–15 mm. Older lobsters (12–24 months old, 22–32 mm carapace length), released in August 1988, were marked by burning small spots in their carapace (Abrahamsson 1965). They were packed in damp transportation boxes and cooled with ice and and arrived at the release location within 18 h. On arrival, lobsters were given a minimum recovery time of 30 min in ambient seawater. They were then released into the sea surface in shallow waters (<10 m). All individuals were released within 3 h of opening the transportation boxes. Transport-related mortality was <5%.

Releases were conducted in summer (May, June, and August) and winter (December, February, March, and April). The release densities at both Langøysundet and Kvitsøy were not more than one lobster per 1 m of running shoreline, as recommended by the Institute of Marine Research research team. However, the fishermen charged with conducting some of the releases often did so at higher densities, especially in areas that they thought were "good lobster places."

Approximately 51 200 juvenile lobsters were released during this study. A total of 10 releases were done: four at Langøysundet, four at Kvitsøy, and two at Huftarøy (Table 1). The releases in Langøysundet consisted of three winter releases totalling 3850 lobsters and one summer release of 2100 lobsters. Winter releases of 35 688 lobsters, from 11 000 to 29 000 juveniles each year, were conducted at Kvitsøy, and two summer releases totalling 9500 lobsters were conducted at Huftarøy.

Winter releases at Kvitsøy were conducted by local lobster fishermen within their own established fishing grounds. Rocky substrates were favoured, but due to the complex and variable bottom topography and the high numbers of lobsters for release, individuals were probably also released onto sand. On one occasion (April 1993), the releasers were instructed to place groups of lobsters on rocky substrate and on sand for comparison (Table 1). Summer releases were not conducted at Kvitsøy. Divers were used occasionally to determine whether predation was a factor during winter releases in March at Kvitsøy and Langøysundet.

For the August 1988 summer release at Huftarøy, lobsters were released at 3–6 m depth onto rocky substrate. They were released directly from the transportation boxes without acclimatisation. Divers observed the lobsters on the bottom for 45–60 min following this release.

The June 1991 release at Huftarøy was conducted to make videorecordings. These lobsters were acclimated to ambient seawater temperature in open trays for at least 1 h and were released one or two at a time over a seaweed-covered sand bottom. A diver with a videocamera was situated on the bottom and recorded both the descent of the lobsters and the activity on the sea bottom. One series of releases was conducted at 1 m depth along a portion of the shore where the sandy and rocky bottom met, while the rest of the releases were at depths of 3 m on sand covered with kelp.

Predator sampling

The predation records and counts of eaten lobsters/lobster tags were made using 59 trammel net hauls, six eel trap hauls, approximately 20 min of videorecordings, and direct observation done by divers (Table 2). Similar trammel nets were available at all locations and were used to provide comparable data on the diversity of swimming organisms and potential predators. Eel traps were used on an occasional basis to fill in catches of bottom-dwelling species too small to be caught in trammel nets but still potential lobster predators. The sampling at Langøysundet was undertaken using trammel nets set during the 24 h after each release. The nets covered more than half of the release area, and the number of nets varied according to the size of the release. The trammel nets were 2 × 28 m with a fine mesh of 70 mm and a coarse mesh of 460 mm.

At Kvitsøy, sampling was done during the 24 h after each lobster release. Due to the complex bottom structures at Kvitsøy, a mixture of the two bottom types could be found nearly everywhere, but the sampling was done by systematic fishing in eight selected areas: four dominated by rocks and four with more sand. Eight trammel nets, similar to those deployed at Langøysundet, were used in the same locations immediately after each release once a month from April 1993 to April 1994. In addition, the one instance from the monthly fishery where a lobster predator was present is included in this paper.

At Huftarøy, predator sampling was on rocks only, with one trammel net and two eel traps deployed at each of the three locations immediately after the release in August 1988 and then once a week for 4 more weeks. The three-chambered eel traps were circular, 1.5 × 0.45 m, with a 3.5 × 0.45 m leading net at the entrance. Mesh size of the leading net and first chamber was 35 mm, 30 mm in the second chamber, and 25 mm in the third chamber. Sampling was undertaken directly on the release sites and not in the surrounding areas.

Surface sea temperature was measured at release or was obtained from routine monitoring established at certain locations. These data were used to evaluate whether sea temperature and lobster predation were correlated.

Statistics

A χ^2 test was used to compare the distribution of numbers of animals from the most important predatory groups in the samples (catch composition) during winter and summer at each location (H_0: no difference in the species composition between summer and winter at any given location). The same test was used to make between-location comparisons (H_0: no difference in the species composition between locations in either winter or summer).

Possible between-season (and bottom substrate) differences in predation were evaluated using the Fisher exact probability test and the χ^2 test. (H_0: no differences in predation on lobsters on rocky and sandy bottom in winter and summer). Each of the release locations was tested separately due to small differences in release technique between teams as well as regional differences in bottom substrates and local fauna.

Spearman rank correlations (r_s) were used to test the relationship between sea temperature and catch (fish and crustaceans) per net per day (CPUE), eaten lobster juveniles or lobster tags per net per day (LPUE), and numbers of individual predators per net per day (PPUE) using data from all three locations (H_0: no differences in catch of fish, number of lobsters eaten, or number of lobsters per predator at different temperatures). The correlations were based on

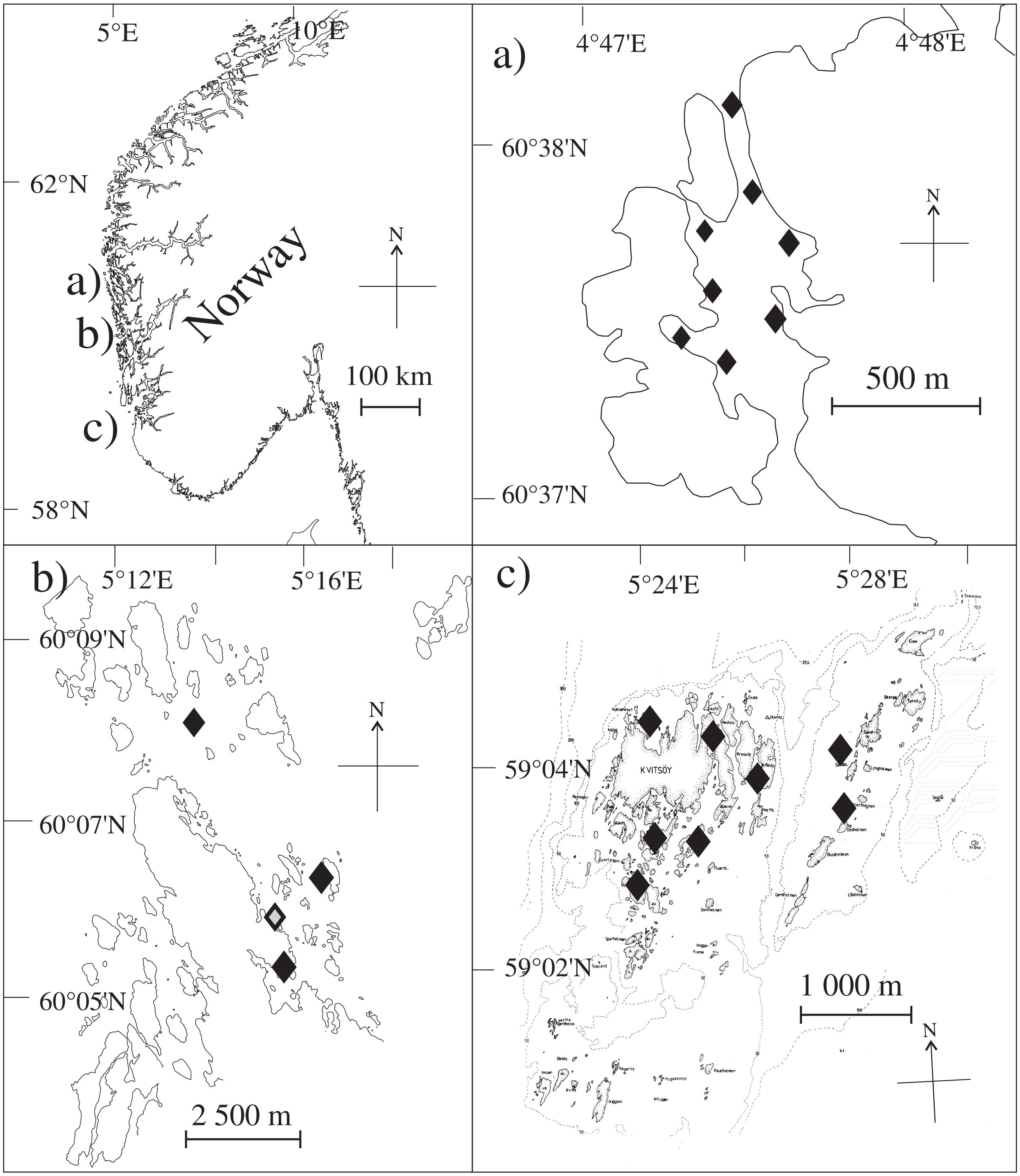


Fig. 1. Map showing (*a*) Langøysundet (4°47′E, 60°38′N), (*b*) Huftarøy (5°14′E, 60°07′N), and (*c*) Kvitsøy (5°26′E, 59°04′N) in south-western Norway. Predator sampling areas are indicated with black diamonds. The grey diamond indicates the videorecording area. In Langøysundet, from three to eight selected areas were fished simultaneously according to the numbers of released lobsters. At Huftarøy and Kvitsøy, all areas were fished simultaneously.

the nine samplings associated with the lobster releases for stock enhancement purposes. The data from June 1991 and June 1993 were therefore omitted.

A one-tailed Student's *t* test on log-transformed size measurements was used to compare the size of Atlantic cod (*Gadus morhua*) with versus without lobster remnants in the gut. In cases for which the size distributions were not normally distributed, the one-tailed Mann–Whitney *U* test was used to evaluate size differ-

Table 1. Numbers of lobsters released and trammel nets used in the predator sampling.

		Lobsters released			Number of nets		
Location	Date	Sum	Rocks	Sand	Sum	Rocks	Sand
Langøysundet	3 Dec. 1992	750	0	750	4	0	4
	25 Feb. 1993	2 100	1600	500	6	4	2
	27 Mar. 1992	1 000	1000	0	6	6	0
	21 May 1992	2 100	1400	700	8	4	4
	Sum	5 950	4000	1950	24	14	10
Huftarøy	24 June 1991	75 – 100	0	75 – 100			16:10 min (video)
	17 Aug. 1988	9 500	9500	0	9	9	0
Kvitsøy	7 Dec. 1993	5 576			8	4	4
	10 Mar. 1994	14 160			8	4	4
	18 Apr. 1994	4 168			8	4	4
	23 Apr. 1993	11 784	5897	5897	8	4	4
	Sum	35 688			32	16	16

ences between other lobster predators and their conspecifics (H_0: individuals that preyed upon lobsters were not different in size from their conspecifics that did not prey upon lobsters).

Results

Season

The summer release at Huftarøy in August resulted in substantial losses of lobsters. When lobsters were released without prior acclimatisation, as in this case, they were either passive for at least 15 min, swimming vertically up and down in the water column, or climbing to the top of rocks and kelp. This was in gross contrast with later releases. When divers inspected parts of the release areas 30 min after release, the acclimatised lobsters had moved into shelter. Only on a few occasions could parts of antennae, claws, or tails be seen.

Divers commonly saw attacks by predators during summer releases, but not winter releases, at Kvitsøy and Langøysundet. The visual impression from Huftarøy was that Labridae were the dominant predators, and massive attacks on lobsters by the wrasse *Labrus bergylta* were recorded in June. Within 16 min, 17 attacks and nine killings were registered. In August 1988, reports from divers described numerous fish, mostly Labridae, attacking and eating lobsters within minutes after the release. At all three locations, divers estimated the immediate loss to be more than 10% of the lobsters within the first hour. Despite the limited fishing effort (Table 1), 0.17% of the released lobsters were found in the stomachs of fish the 24 h following the release (Table 2). Divers also reported crushed lobsters in Labridae feces at one of the release locations the next day, but no live lobsters. A significantly higher fraction of the released lobsters were eaten after the summer release at Langøysundet compared with winter releases at the same location ($\chi^2 = 13.203$, df = 1, $p < 0.0001$). Relative to the numbers of lobsters released in winter at Kvitsøy and Langøysundet, less lobsters were found eaten at Kvitsøy than at Langøysundet, 0.02 and 0.16%, respectively (Tables 1 and 2).

Sea temperature, CPUE, LPUE, and PPUE were not correlated (CPUE: $r_s = 0.185$, $n = 9$; LPUE: $r_s = 0.411$, $n = 9$; PPUE: $r_s = 0.377$, $n = 9$) (Fig. 2).

Bottom substrate

Significantly higher numbers of lobsters were found eaten by fish and crustaceans caught on sand than on rocks, both at winter releases at Langøysundet (73.7%; Fisher exact probability test, $p = 0.0012$) and at Kvitsøy (87.5%; Fisher exact probability test: $p < 0.0001$). The predation in the summer at Langøysundet, as recorded from stomach analyses, and the visually observed predation at Huftarøy occurred with much less difference both on rocks and on sand (August 1988 and June 1991; Fisher exact probability test, $p = 0.814$) (Table 2).

Predators

The highest CPUE in the trammel net fishery occurred in the summer, with 32.5 at Kvitsøy and 13.3 at Hufthamar (Fig. 2). CPUE at Langøysundet fluctuated between 4.2 and 13.0, but both the highest and lowest CPUE were after winter releases. CPUE at Kvitsøy in winter were similar to those at Langøysundet and went from 5.8 to 11.9.

In winter, LPUE and PPUE were one to one, except for a December release at Langøysundet, while in summer, LPUE were higher than PPUE (Fig. 2). This difference was mainly due to three predatory species, *L. bergylta*, *G. morhua*, and European flounder (*Platichthys flesus*), often found with two or more lobsters eaten per fish. Usually, only one lobster per predator was found after winter releases, except for two lobster tags found in one shorthorn sculpin (*Myoxocephalus scorpius*) stomach in April 1993 and six lobsters found in one *G. morhua* stomach in December 1992. No correlation between the size of the released lobsters and that of the eaten lobsters could be made due to the conditions of the eaten lobsters, being crushed and more or less digested by the predator.

Of the 32 species registered in the predator sampling, 29 were caught in the summer and 24 in the winter (Table 3). Nine of these species, mainly the Labridae, showed predator

Table 2. Captures of fish and crabs that had eaten lobsters and numbers of eaten lobsters recovered.

		Predators			Eaten lobsters		
Location	Date	Sum	Rocks	Sand	Sum	Rocks	Sand
Langøysundet	3 Dec. 1992	1	0	1	6	0	6
	25 Feb. 1993	0	0	0	0	0	0
	27 Mar. 1992	0	0	0	0	0	0
	21 May 1992	6	3	3	13	5	8
	Sum	7	3	4	19	5	14
	Frequency		42.9	57.1		26.3	73.7
Huftarøy	24 June 1991	15*	0	15*	9*	0	9*
	17 Aug. 1988	8	8	0	16	16	0
	Sum	>23	8	>15	25	16	9
	Frequency		34.8	62.5		64.0	36.0
Kvitsøy	7 Dec. 1993	1	0	1	1	0	1
	10 Mar. 1994	1	0	1	1	0	1
	18 Apr. 1994	4	1	3	5	1	4
	23 Apr. 1993	1	0	1	1	0	1
	Sum	7	1	6	8	1	7
	Frequency		14.3	85.7		12.5	87.5
All locations	Sum	>37	12	>25	52	22	30
	Frequency		32.4	67.6		42.3	57.7

Note: Videorecordings are marked with an asterisk. Numbers of predators were in this case not certain due to the limited frame of the videocamera. Sum is the total numbers, in each region and totally, of lobster predators and eaten lobsters recovered. Frequency is the fraction of lobster predators and eaten lobsters recovered from captures in rocky and sandy habitat.

activity only in the summer. Although the crab *Cancer pagurus* and *M. scorpius* were registered as predators only in the winter, they were found in the catches year-round. Yet 71.4% (n = 5) and 96.0% (n = 48) of *M. scorpius* from Langøysundet and Kvitsøy, respectively, were landed in the winter, indicating a high winter activity of this species (Table 4). Only two species, *G. morhua* and the crab *Carcinus maenas*, were found as active predators in both seasons. In March, the only predator recorded was *M. scorpius*, even though more than 17 000 lobsters had been released at two locations.

The summer sampling from Huftarøy and Langøysundet showed no significant differences in species composition (χ^2 = 0.4702, df = 2, p > 0.05) (Table 4). The difference in sampled species composition between summer and winter was highly significant, both at Langøysundet (χ^2 = 64.370, df = 2, p < 0.0001) and at Kvitsøy (χ^2 = 276.630, df = 2, p < 0.0001). While the Labridae dominated in numbers in the summer, the Gadoidae and crustaceans were most numerous in the winter. The very high density of Labridae at Kvitsøy, compared with Langøysundet/Huftarøy, gave a significant difference between sampled species composition at Kvitsøy and at the other locations (χ^2 = 9.014, df = 2, p < 0.025). The difference in species compositions between Langøysundet and Kvitsøy was even greater in winter, when the Gadoidae dominated at Langøysundet, while crustaceans and Cottidae were most numerous at Kvitsøy (χ^2 = 61.897, df = 4, p < 0.001).

Juvenile lobsters were usually not found eaten at times other than the day of release at Huftarøy or Kvitsøy. The two possible exceptions were at Kvitsøy, where one lobster released in April was later recognised by the tag in an adult lobster delivered by fishermen 1 month after release and one tag found in an *L. bergylta* more than 2 months after release.

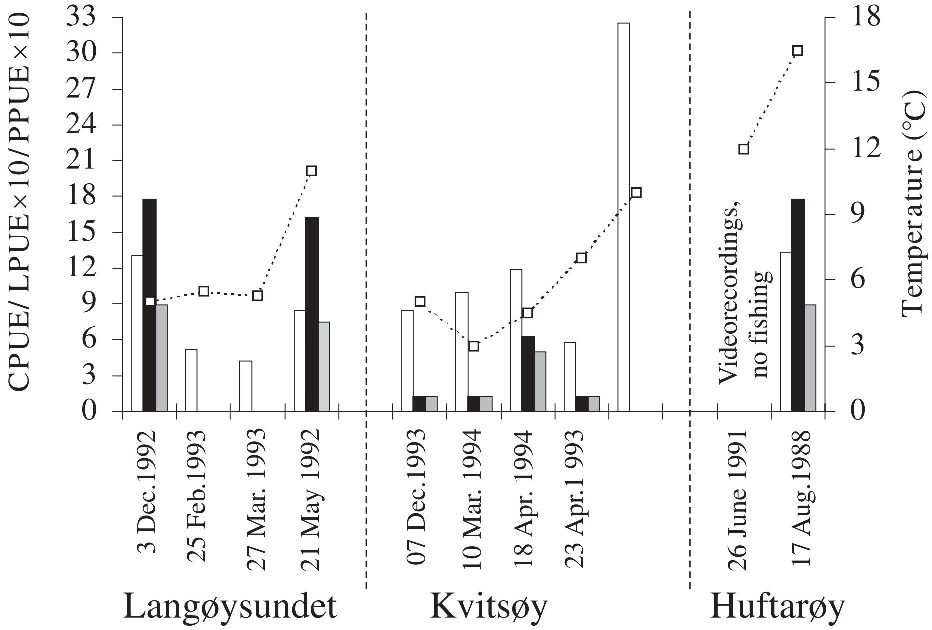
The predator size was usually between 15 and 40 cm (Table 5). Most predators did not differ significantly in size from other individuals of their species, but exceptions were seen. In the wrasse *Labrus mixtus*, all predators were females and were significantly smaller than the males and females with no lobster remnants in the stomach (one-tailed Mann–Whitney U test, p = 0.022). The wrasse *Crenilabrus melops* predators had a tendency to be among the smaller of that species (one-tailed Mann–Whitney U test, p = 0.058), while the wrasse *Ctenolabrus rupestris* tended to be among the larger, although not significantly so (one-tailed Mann–Whitney U test, p = 0.058). The two predatory poor cod (*Trisopterus minutus*) caught were both larger than the rest encountered.

Discussion

Release and sampling techniques

When releasing juvenile lobsters after transportation in cool, damp boxes, acclimatisation to ambient sea temperature is vital to keep the lobsters awake and alert and walking forwards while using the claws and antennae to investigate potential shelters (van der Meeren 1991). However, even when acclimatised and released at the sea bottom instead of the sea surface, summer releases continued to result in higher lobster mortality than winter releases. The most plausible cause for the difference in mortality is found in the predator species composition in summer and winter. The

Fig. 2. CPUE (open bars), as fish/crustaceans per fishing gear, in the first 24 h after the releases of juvenile lobsters. For comparison, LPUE (solid bars) and PPUE (shaded bars) are also presented and are multiplied by 10 to fit onto the graph. Temperature (squares) at the release dates are shown, to see if predation might be temperature dependent. Trammel nets were used for predator fishing, while eel traps were used in addition at Huftarøy.



high density of Labridae in summer makes the risk of loss of newly released lobsters to predators much higher than in winter. Mortality could also be due to temperature-enhanced lobster activity, resulting in reduced shelter use and increased predator exposure (van der Meeren 1993), but this is less likely. Shelter use in juvenile American lobster (*Homarus americanus*) is sensitive to predators (Wahle 1992*b*). Underwater observations and videorecordings showed that the acclimatised lobsters were seeking shelter within a few minutes after release even in the winter. No acclimatised lobsters could be seen on the sea bottom by divers 30 min after release at any time of the year.

The magnetic steel tag in a released lobster made it easily identifiable even in the stomach of a live fish when checking the catch with a tag detector. Even when the lobster had been dissolved, the tag would reveal age and origin of the lobster. Due to the tags, the quantification of lost lobsters in the samples should be reliable, although it might be underestimated due to lobsters and tags being discarded from the predators before examination. Lobster remnants in Labridae feces were observed less than 24 h after the release in August.

Bottom substrate and season

Even though the samplings were not designed to catch all the lobster predators but to present a subsample of the present fauna, this study showed that both the time of year and the bottom substratum are of importance for survival of newly released juvenile lobsters. The distribution of predators could be confused by fish swimming between the bottom types. Yet significantly more predators were captured on sand in winter, in spite of the fact that most of the lobsters were released onto rocks, and one of the important winter predators, Cottidae, is known to be a rock-preferring species (Pethon 1985). This difference in lobster predation between rocks and sand was not found in summer, but that might be due to the change in predator species from bottom-dwelling fish to more mobile species. The Labridae, visually observed when eating lobsters in the summer, seemed to be attracted into the release area. It could also be due to the feeding activity of conspecifics, by the presence of the lobsters, or by the human activity in connection to the releases. Specific substrates, usually cobble grounds, are important nursery grounds for juvenile *H. americanus* (Wahle and Steneck 1991; Wahle 1992*a*, 1992*b*). The vulnerability of juvenile lobsters out of shelter has been demonstrated in *H. americanus* (Lavalli and Barshaw 1986; Barshaw and Lavalli 1988; Wahle and Steneck 1992) and also recently in *H. gammarus* (Mercer et al. 2000).

Except for two cases, all the eaten lobsters in this study were found within 24 h after release. This indicates that predators are a hazard mainly to lobsters immediately after release, before they are established within shelters. The major predator groups of *H. americanus* are similar to the predators found in this study, with Labridae, Cottidae, and crustaceans being the most important predatory taxa. In addition, this study found that the Gadoidae were among the important predators. More species than those presented here have been observed attacking tethered early benthic lobsters in European waters (Mercer et al. 2000).

A remaining unsolved problem is to find the optimal shelter habitats for juvenile *H. gammarus*. Distribution of settling juveniles in several Brachyura species is caused by habitat selection (Eggleston and Armstrong 1995; Hedvall et al. 1998). Wild juveniles have never been found in Europe either in cobble or in any other habitat (Mercer et al. 2000). On the other hand, the fauna living in cobble grounds in Europe is much more diverse than that in North America (Wahle 1998; Mercer et al. 2000). To develop successful

Table 3. Fauna composition during times of lobster predation.

Species	Dec.[a,b]	Feb.[a]	Mar.[b]	Apr.[b]	May[a,c]	June[b,d]	Aug.[d]
Cancer pagurus	Black			Black		Grey	Grey
Gadus morhua	Black	Grey	Grey	Grey	Black	Grey	Grey
Myoxocephalus scorpius	Grey	Grey	Black	Black	Grey	Grey	Grey
Trisopterus minutus	Grey	Grey					Black
Carcinus maenas	Grey		Grey	Black		Black	Black
Ctenolabrus rupestris	Grey			Grey	Grey	Grey	Black
Labrus mixtus	Grey				Black	Grey	Black
Crenilabrus melops	Grey				Grey	Grey	Black
Platichthys flesus			Grey		Black		
Labrus bergylta				Grey	Black	Black	Black
Homarus gammarus				Grey	Black		
Anguilla anguilla							Black
Gobius niger							Black
Pollachius pollachius	Grey	Grey	Grey	Grey	Grey	Grey	Grey
Pollachius virens	Grey	Grey		Grey	Grey	Grey	Grey
Galathae spp.	Grey		Grey	Grey			
Agonus cataphractus	Grey				Grey	Grey	
Lithodes maja	Grey						
Pleuronectes platessa		Grey		Grey			
Cyclopterus lumpus		Grey	Grey	Grey		Grey	
Microstomus kitt			Grey	Grey			
Lycodes vahlii			Grey	Grey		Grey	
Hyas araneus			Grey	Grey			
Clupea harengus			Grey				Grey
Pagurus spp.				Grey			
Anarhicas lupus				Grey			
Callionymus lyra					Grey		
Trachinus draco					Grey		
Merlangius merlangus					Grey		Grey
Pomatoschistus minutus							Grey
Raniceps raninus							Grey
Centrolabrus exoletus							Grey

Note: Grey box, species registered; black box, species registered as lobster predators (lobsters/lobster tags in the stomach or mouth); open box, species not registered. Sampling methods were
[a]Trammel nets at Langøysundet.
[b]Trammel nets at Kvitsøy.
[c]Lobster pots at Kvitsøy.
[d]Diver observations, eel traps, and trammel nets at Huftarøy.

lobster release programmes anywhere, it is important to describe the best habitats for juvenile stages in order to offer released juveniles the best possibilities for survival.

Predators

Potential predators were probably missed due to low fishing intensity in relation to the area into which the lobsters were released, gear selectivity, choice of fishing location, or low density of that species compared with fishing effort. Some species might also be potential predators on lobsters of a size another than that of the released lobsters. The lobsters released were all relatively large juveniles in the early benthic phase and some near transition to the adolescent phase in August 1988. *Ctenolabrus rupestris* and *T. minutus* found as predators after this release tended to be among the larger of these species. It is plausible that smaller sized fish of both species would succeed in eating smaller lobsters than the released ones. The data set assembled in this study was not fit for statistical tests of the relationship between predator and lobster size. The lobsters were produced to meet the standard set by the Institute for Marine Research for stock enhancement purposes and not for qualitative ecological experiments. In addition, even if lobsters of various sizes were released, the remnants recovered were usually only the tags or too fragmented to be remeasured. Despite methodical flaws in order to get a more detailed picture of potential lobster predators, our documented predator list presents a series of important predators in European waters, where some are seasonally present in sufficient numbers to negatively impact the survival of released lobsters.

The Labridae, known as an important group of shallow-water predators in tropical and temperate waters (Wahle and Steneck 1992), include the most numerous fish species in Nordic European shallow waters in the summer (Hildén 1984). Representatives of this fish family were found to be the most important lobster predators in this study. These species are active only in summer and autumn in temperate waters, leaving the shallow waters in the winter (Hildén 1984).

Table 4. Comparisons of occurrence between the four major predatory families and a fifth group, mainly composed of flatfish and eels, as total number of animals caught at each release location in the summer and winter.

	Labridae	Gadoidae	Cottidae	Decapoda	Other	Sum
Langøysundet (winter)	7	63	5	28	5	108
Predators (%)	0	1.6	0	0	0	0.9
Kvitsøy (winter)	12	36	48	102	10	208
Predators (%)	0	0	8.3	2.9	0	3.4
Langøysundet (summer)	41	18	2	0	6	67
Predators (%)	9.8	5.6	0	0	16.7	9.0
Huftarøy (summer)	86	37	1	4	7	135
Predators (%)	11.6	5.4	100	25	28.6	11.9
Kvitsøy (summer)[a]	192	57	2	7	2	260
Predators (%)	0.5	0	0	0	0	0.4

Note: The frequency of active lobster predators within each group is shown for each region.
[a]The summer sampling at Kvitsøy was not related to a lobster release.

Table 5. List of predatory fish species, with mean size, SD, and numbers of documented predators and as well as the rest of catch of the same species.

	Predators			Others		
Species	Size (mm)	SD	*n*	Size (mm)	SD	*n*
Labrus bergylta	280.0	60.0	4	271.6	61.3	81
Labrus mixtus	208.0	14.4	6	245.3	33.7	103
Crenilabrus melops	172.5	2.5	2	187.3	12.9	110
Ctenolabrus rupestris	180.0	0	1	132.1	18.8	24
Gadus morhua	280.0	50.0	2	347.1	77.3	95
Trisopterus minutus	300.0	0	2	200.0	0	2
Myoxocephalus scorpius	193.3	31.1	4	193.3	26.5	71
Anguilla anguilla	550.0	0	1	560.0	50.0	2
Gobius niger	150.0	0	1	150.0	0	1
Platichthys flesus	360.0	0	1	345.0	35.0	2

The Labridae are more or less dependent on rocky substratum (Hildén 1984), like the habitat into which many of the lobster were released. Sand occurs in patches within and below rocky shores, well within the swimming range of the Labridae, in most places along the Norwegian coast. Four out of five Labridae species were lobster predators, and *L. bergylta* and *L. mixtus* had usually eaten more than one lobster per fish. In this study, most of the Labridae were between 10 and 50 cm. The larger sized species *L. bergylta* and *L. mixtus* are both known to mainly consume decapod crustaceans. Why only female *L. mixtus* were found to be predatory might be due to the territorial males being busy fending off nonterritorial intruders, attracted into their territory by the lobster release, or to size-selective feeding by the smaller females. *Labrus mixtus* is hermaphroditic, and large dominant females in the harem turn into males after the territorial males disappear (Hildén 1984). The smaller Labridae species mainly consume amphipods and copepods (Hildén 1984) but can be expected to be predators on smaller juvenile lobsters than those released in this study.

The second important predator, *G. morhua*, is common along the Norwegian coast throughout the year (Pethon 1985). Most of the specimens caught during this study did not contain any lobsters or lobster remnants. However, the ones that did prey on lobsters had eaten several lobsters per fish. If lobsters released in high densities can induce search selectivity in these highly mobile predators, the potential for substantial loss of lobsters is high.

Crustaceans, like the Brachyura *C. pagurus* and *C. maenas*, are commonly found along the Norwegian coast (Christiansen 1969). They are known to have temperature-dependent activity, being active in the summer (Naylor 1963; Crothers 1968; Karlsson and Christiansen 1996). Yet, predation on juvenile lobsters was seen in the spring, summer, and winter. Still, the number of lobsters taken by crustacean predators was low. The videorecorded crab attacks showed that lobsters had to walk in close to the crab before the crab attacked. Crab predation was recorded on sand, but crabs can catch juvenile lobsters on rocky substrate also (Lavalli and Barshaw 1986). Predation by crabs might be cumulative over time; since they can also forage within rocky shelters, they can probably catch shelter-living lobsters in the weeks and months after the release. In addition, intraspecific competition and predation in newly settled and juvenile Brachyura species, which in many ways are comparable with lobsters, are the most common regulation of population size besides refuge habitats (Kurihara and Okamoto 1987; Pile et al. 1996; Moksnes 1999). This also seems to be true for the European lobster (Mercer et al. 2000). Long-term mortality due to intra- and inter-specific predation needs further study.

Myoxocephalus scorpius was the only species to be active as a predator mainly in the winter. One individual of this species was the only predator registered after the release of 17 000 juvenile lobsters in February–March. Due to the low density and its sit-and-wait foraging tactic, it will probably not contribute to lobster mortality in winter at the same scale as the Labridae do in the summer.

The small-sized members of the fish families Gobiidae, Blennidae, and Pholidae as well as *C. maenas*, *Liocarcinus arcuatus*, and other portunid and xanthid crabs are representative of known and potential predators living in the shallow waters of Europe, presenting a threat to early benthic phase lobsters, at least when the lobsters are out of shelter (Mercer et al. 2000). Rearing the lobsters to more than 15 mm carapace length might protect them from smaller fishes and crustaceans, but they are still vulnerable to predatory fishes longer than 15–18 cm. Due to the high density of the Labridae from May to October, releases of lobsters during this period can be expected to induce high mortality in the lobsters. Predator-deterrent actions could be carried out in order to diminish the numbers of predators from a location prior to releasing the lobsters. Large-scale fishing operations to remove the numerous Brachyura and Labridae living along the coast may disrupt local ecosystems and create unwanted ecological side effects. In addition, if the predators are of commercial importance themselves, such as *G. morhua* and the Labridae in some regions of Norway, removal of the fish will create conflicts with local fisheries. Since the lobsters seem to be quite safe from fish predators as soon as they find shelter, it is not necessary to remove the fish permanently. One tempting, but not tested, solution might be to scare the predators temporally away by the use of acoustic soundings a short time before the release at the chosen location (E. Ona, Institute of Marine Research, P.O. Box 1870, N-5817 Bergen, Norway, personal communication).

The numbers of lobsters found in fish and invertebrate predators in this study were quite low. When divers estimated the loss after an August release to be more than 10%, the recollection of juveniles from fish stomachs was only 0.17%. The present quantity of predated lobsters must therefore be regarded as subsamples and should not be expected to represent the total loss within 24 h from release. The actual loss could be up to 100 times the observed 0.17% mortality based on stomach contents. In addition longer term mortality must be expected, even if it was not identified in this study. Because little is known of the natural abundance of European lobsters (Mercer et al. 2000), it is difficult to make recommendations on optimal lobster juvenile density to avoid intraspecific competition and predation, but the new knowledge of predators on newly released lobster juveniles can be used to refine release techniques.

Even if the release techniques used so far were crude and based on guessing more than on fact, recaptures of both winter- and summer-released lobsters do occur regularly today. Relatively high numbers of released lobsters are landed compared with wild lobsters in the commercial lobster fishery of Kvitsøy 3–10 years after the release (van der Meeren and Næss 1991; Tveite and Grimsen 1995; Agnalt et al. 1999) but not enough to make it economically feasible. As long as the production price is more than 1£ per released lobster juvenile, loss of juvenile lobsters must be minimised to make the releases economically viable (Borthen et al. 1999).

Based on the present results and previous experience from lobster releases in Norway, the recommendations for when and where to release juvenile lobsters are as follows.

(*i*) Make a faunal investigation of the chosen release location by monitoring the fish and crustacean species in the area a full year prior to release. This should be done to be able to conduct the releases at the time of year for release when seasonally active predators are not present. In Nordic waters, the releases should be carried out in late winter – early spring to avoid loss due to the summer-active Labridae.

(*ii*) Release the juvenile lobsters on a substratum that offers sufficient shelter. Rocky bottoms are expected to be suitable, as long as they offer many crevices. Even if the diversity of other crustaceans and small fish is high in such habitats, the alternative sandy bottoms with no shelters have been found to result in higher loss to predators.

(*iii*) Predator-deterrent actions should not harm existing commercially and ecologically important species in the area to avoid conflicts with local fisheries and the possibility of disruption of the ecosystem supporting the commercial stocks.

Until more knowledge on the ecology of *H. gammarus* is available, the recommendations for where and when to release juvenile lobsters must be given with precautions, and further studies will be needed to confirm or refine the recommendations suggested.

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References

Abrahamsson, S.A.A. 1965. A method of marking crayfish *Astacus astacus* Linné in population studies. Oikos, **16**: 228–231.

Addison, J.T., and Bannister, R.C.A. 1994. Re-stocking and enhancement of clawed lobster stocks: a review. Crustaceana (Leiden), **67**: 131–155.

Agnalt, A.-L., van der Meeren, G.I., Jørstad, K.E., Næss, H., Farestveit, E., Nøstvold, E., Korsøen, E., Ydstebø, L., and Svåsand, T. 1999. Stock enhancement of European lobster (*Homarus gammarus*); a large-scale experiment off southwestern Norway (Kvitsøy). *In* First Symposium on Stock Enhancement and Sea Ranching. *Edited by* B. Howell, E. Moksness, and T. Svåsand. Blackwell Scientific Publications, London, U.K. pp. 401–419.

Appelöf, A. 1909. Undersøkelser over hummeren (*Homarus vulgaris*) med særskilte hensyn til dens optræden ved Norges kyster. Aarsberetning vedkommende Norges fiskerier. 1ste hefte. Særtrykk, A.S. John Griegs Boktrykkeri, Bergen.

Bannister, R.C.A., Addison, J.T., and Lovewell, S.R.J. 1994. Growth movement recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* Linnaeus, (1758)) released in the wild on the English east coast. Crustaceana (Leiden), **67**: 156–186.

Barshaw, D.E., and Lavalli, K.L. 1988. Predation upon postlarval lobster *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crab *Neopanope sayi* on three different substrates: eelgrass, mud, and rocks. Mar. Ecol. Prog. Ser. **48**: 119–123.

Borthen, J., Agnalt, A.-L., Nøstvold, E., and Sørensen, J. 1998. Havbeite med hummer. Norges forskningsråd, Oslo, Norway.

Borthen, J., Agnalt, A.-L., and van der Meeren, G.I. 1999. Lobster stock enhancement in Norway — "Lobst. eco" — a bioeconomic model. Presenting of model and evaluation of some main results. *In* First Symposium on Stock Enhancement and Sea Ranching. *Edited by* B. Howell, E. Moksness, and T. Svåsand. Blackwell Scientific Publications, London, U.K. pp. 583–596.

Christiansen, M.E. 1969. Crustacea Decapoda Brachyura. Universitetsforlaget, Oslo, Norway.

Crothers, J.H. 1968. The biology of the shore crab *Carcinus maenas* (L.). 2. Life of the adult crab. Field Stud. **2**: 579–614.

Dannevig, A. 1928. The rearing of lobster larvae at Flødevigen. Rep. Norw. Fish. Mar. Invest. **3**: 1–15.

Eggleston, D.B., and Armstrong, D.A. 1995. Pre- and post-settlement determinantes of estuarine dungeness crab recruitment. Ecol. Monogr. **65**: 193–216.

Grimsen, S., Jaques, R.N., Ernest, V., and Balchen, J.G. 1987. Aspects of automation in a lobster farming plant. Model. Identif. Control, **8**: 61–68.

Hedvall, O., Moksnes, P.-O., and Phil, L. 1998. Active habitat selection by megalopae and juvenile shore crabs *Carcinus maenas*: a laboratory study in an annular flume. Hydrobiologia, **375/376**: 89–100.

Hildén, N.-O. 1984. Behavioural ecology of the labrid fishes (Teleostei: Labridae) at Tjärnö on the Swedish west coast. Ph.D. thesis, Department of Zoology and Tjärnö Marine Biological Laboratory, University of Stockholm, Stockholm, Sweden.

Howard, A.E. 1983. The behaviour of hatchery reared juvenile lobsters (*Homarus gammarus*), released and observed by divers. ICES CM 1983/K:3.

Jefferts, K.B., Bergman, P.K., and Fiscus, H.F. 1963. A coded wire identification system for macro-organisms. Nature (Lond.), **198**: 460–462.

Karlsson, K., and Christiansen, M.E. 1996. Occurrence and population composition of the edible crab (*Cancer pagurus*) on rocky shores of an inlet on the south coast of Norway. Sarsia, **81**: 307–314.

Kurihara, Y., and Okamoto, K. 1987. Cannibalism in a grapsid crab, *Hemigrapsus penicillatus*. Mar. Ecol. Prog. Ser. **41**: 123–127.

Latrouite, D., and Lorec, J. 1991. L'expérience française de forçage du recrutement du Homard Européen (*Homarus gammarus)*: résultats préliminaires. ICES Mar. Sci. Symp. **192**: 93–98.

Lavalli, K.L., and Barshaw, D.E. 1986. Burrows protect postlarval lobsters *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus*, but not from the burrowing crab *Neopanope texani*. Mar. Ecol. Prog. Ser. **32**: 13–16.

Mercer, J.P., Bannister, R.C.A., van der Meeren, G.I., Debuse, V., Mazzoni, D., Linnane, A., and Ball, B. 2000. The influence of competitive interactions on the abundance of early benthic stage European lobster (*Homarus gammarus* (L.)) and hence on the carrying capacity of lobster habitat. Final report LEAR FAIR CT-96-1775 (draft). Shellfish Research Laboratory, Carna, Co. Galway, Ireland. pp. 1–158.

Moksnes, P.-O. 1999. Recruitment regulation in juvenile shore crabs *Carcinus maenas*: importance of intraspecific interactions in space limited refuge habitats. M.Sc. thesis, Göteborg University, Göteborg, Sweden.

Naylor, E. 1963. Temperature relationships of the locomotory rhythms of *Carcinus*. J. Exp. Biol. **40**: 669–679.

Pethon, P. 1985. Aschehougs Store Fiskebok. Aschehoug, Oslo, Norway.

Pile, A.J., Lipcius, R.N., van Montfrans, J., and Orth, R.J. 1996. Density dependent settler–recruit–juvenile relationship in blue crabs. Ecol. Monogr. **66**: 277–300.

Tveite, S., and Grimsen, S. 1995. Survival of one year old artificially raised lobsters (*Homarus gammarus*) released in southern Norway. ICES Mar. Sci. Symp. **199**: 73–77.

van der Meeren, G.I. 1991. Out-of-water transportation effects on behaviour in newly released juvenile Atlantic lobsters, *Homarus gammarus*. Aquacult. Eng. **10**: 55–64.

van der Meeren, G.I. 1993. Initial response to physical and biological conditions in naive juvenile lobsters *Homarus gammarus*. Mar. Behav. Physiol. **24**: 79–92.

van der Meeren, G.I., and Næss, H. 1991. Recatches of marked lobsters, *Homarus gammarus*, released in 1988. ICES CM 1991/K:7.

Wahle, R.A. 1992*a*. Substratum constraints on body size and the behavioral scope of shelter use in the American lobster. J. Exp. Mar. Biol. Ecol. **159**: 59–75.

Wahle, R.A. 1992*b*. Body-size dependent anti-predator mechanisms of the American lobster. Oikos, **65**: 52–60.

Wahle, R.A. 1998. A trans-Atlantic perspective on *Homarus* recruitment and enhancement. *In*: The European lobster *Homarus gammarus* (L.). Proceedings from the seminar at Kvitsøy 1995. Fisken Havet, **13**: 36–43.

Wahle, R.A., and Steneck, R.S. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck. Mar. Ecol. Prog. Ser. **69**: 231–243.

Wahle, R.A., and Steneck, R.S. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. **157**: 91–114.

Wickins, J.F., Beard, T.W., and Jones, E. 1986. Microtagging cultured lobsters for stock enhancement trials. Aquacult. Fish. Manage. **17**: 259–265.