Growth, reproductive cycle, and movement of berried European lobsters (*Homarus gammarus*) in a local stock off southwestern Norway

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The Norwegian fishery for the European lobster (*Homarus gammarus*) collapsed between 1960 and 1980, to <10% of its pre-1960 level, and since then the spawning stock seems to be too low to generate good recruitment. In 1998, a project to evaluate the feasibility and effect of protecting berried female lobsters as a management restriction was initiated. The study area selected was previously an important fishing ground in Kvitsøy off southwestern Norway, and 125 000 hatchery-reared juveniles were released between 1990 and 1994. From spring 1998 to spring 2000, a total of 942 wild and 480 cultured berried females was purchased from fishers, individually tagged with a streamer-tag, and released. The proportion of berried females in the landings varied annually from 19 to 58% for wild females, and from 22 to 44% for cultured females. By spring 2000, 23% of the tagged females had been recaptured at least once, and 3% twice or more. Average moult increment was 7 mm carapace length (CL), independent of pre-moult size in both wild and cultured females. Reproduction (spawning) and growth (moulting) alternated in a 2 y cycle for >90% of the females. A small number moulted and spawned a few weeks after hatching. More than 95% of the recaptures were taken within a radius of 1 km of the release area. Egg production varied considerably between seasons. Reproductive potential (RP) of landed berried females underestimated egg production compared with what was actually produced (AE). For the entire period, RP was estimated to be about 15.0 million eggs, and AE to be 17.2 million eggs. Cultured females contributed 27% of AE. To reduce the fishing mortality in a heavily fished and depleted population is vital. A ban on landing berried females would be a valuable first step in attempting to increase the spawning biomass.

Keywords: egg production, European lobsters, growth, management, movement, reproduction.

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Introduction

The European lobster (*Homarus gammarus*) used to be an important resource with great economic value to many coastal communities in Norway. In good years, before the 1950s, landings fluctuated between 500 and 1000 t annually. Norway was at that time one of the main suppliers of lobsters to the European market, accounting for 24% of total landings (Dow, 1980). From 1960–1980, landings declined dramatically to <10% of the pre-1960 level (Figure 1). Stock size and recruitment has since remained low (Tveite, 1991).

Because of low landings during the 1980s, the industry was keen to investigate stock and fishery enhancement. The Tiedeman company was the main force behind the establishment of a lobster hatchery in mid-Norway in the early-1980s (Tveite and Grimsen, 1995), but the lack of legal ownership and recapture rights forced this enterprise to abandon sea ranching. Then, in 1990, a research programme was initiated, focusing on large-scale releases to enhance or restock the much-reduced local lobster population. From 1990 to 1994, some 128 000 micro-tagged juvenile lobsters were released at Kvitsøy, a 6 km^2 archipelago in Rogaland County, southwestern Norway (Agnalt *et al.*, 1999, 2004). The region was historically one of the main lobster fishing grounds, but suffered from a decline in landings similar to that experienced by Norway in general (Figure 1). Since 1992, commercial landings in the release area were monitored for the presence of cultured survivors. By the end of 1997, 7 y after the first release, it was evident that the landings had increased significantly as a consequence of the releases (Agnalt *et al.*, 1999).

The results of the stock-enhancement programme generated discussions among fishers on management restrictions; there was a general interest to protect and increase the spawning stock. During an annual meeting between fishers, representatives from the local municipality and from the Directorate of Fisheries, and researchers from the Institute of Marine Research in February 1998, a ban on landing berried females was proposed. However, because of national regulations, this could not be legally enforced, so the Directorate of Fisheries funded a 3 y cooperative project. Berried females were bought from fishers during the commercial fishing season, tagged, and released into the area where they had been caught.

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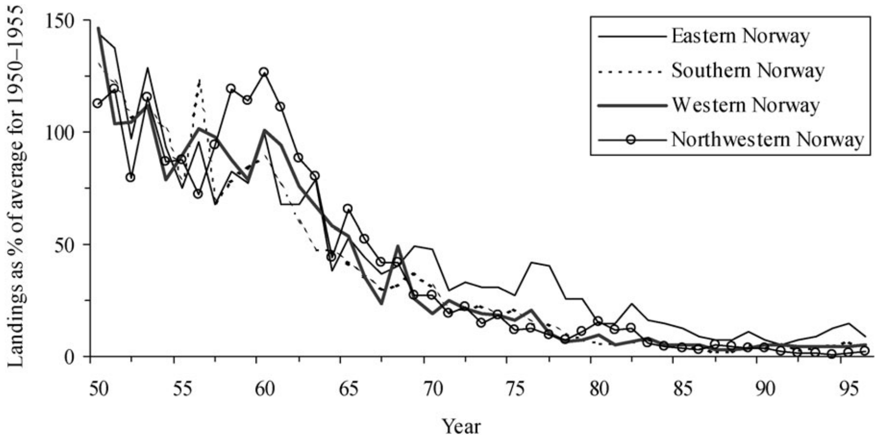

Figure 1. Landings of European lobster (*H. gammarus*) in Norway expressed as the percentage of the average number landed in the period 1950 – 1955.

The objective of this work was to investigate the ban on landing berried females in terms of growth, reproductive cycle, egg production, and migration, for both wild and cultured female lobsters off southwestern Norway. The findings are the first published on a lobster population off western Norway, and they are important in a stock assessment perspective as part of future management. Moreover, comparisons to assess whether cultured lobsters behave the same as wild lobsters are significant from a stock-enhancement perspective.

Material and methods

Berried females were bought from fishers at the Kvitsøy islands (Figure 2), the price being based on the market price in 1998 and 1999. However, by spring 2000 an agreement had been reached with fishers to purchase them at half the market price, which had more than doubled by that time. Minimum legal size in the area is 88 mm carapace length (CL), but berried females <88 mm were also sampled, without payment to the fishers, to obtain as much biological information as possible. The commercial fishing season opens on 1 October and ends on 31 May, but because of low winter temperatures (when lobsters are inactive), the fishery is concentrated in autumn and spring and fishing activity generally ceases from January to March. In autumn, >95% of the landings are made during October and November, and in spring, >85% of the harvest is landed in May.

Total length (TL), CL, carapace width, and abdominal width were measured to the nearest millimetre, and body weight was measured in grammes. The micro-tagged released cultured or ranched females (i.e. hatchery-reared and released as juveniles) were identified by a metal detector (Agnalt *et al.*, 1999, 2004). Berried females were tagged with an individually numbered streamer tag (Hallprint Ltd) inserted on the ventral side through the two ventral abdominal muscles (Figure 3). Tagging was done during spring (May) and autumn (October and November), in the commercial fishing season. Only hard-shelled lobsters were tagged. After tagging, they were kept in a large holding facility in the sea (15 × 45 m, depth 2–4 m) until the end of the fishing

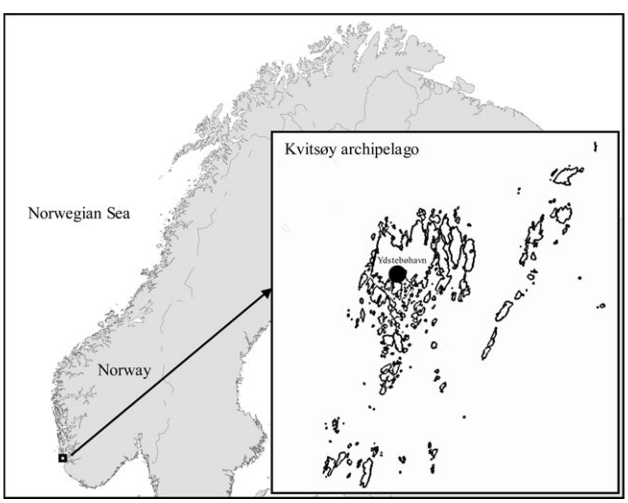

Figure 2. The study site, Kvitsøy archipelago, located in southwestern Norway.

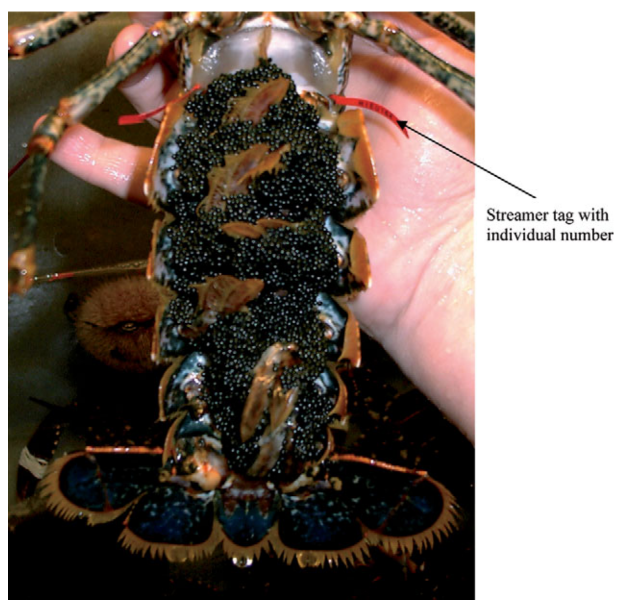

Figure 3. A ventral view of a streamer-tagged ovigerous female lobster.

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season, to preclude immediate recapture. A reward of 25 Norwegian kroner was offered for each recaptured stream-tagged lobster. The release of berried females terminated after spring 2000, but monitoring of streamer-tagged female recaptures continued during the 2000 autumn fishery. Further, tagged berried females were kept in the holding facility on two occasions for about six months, to check for tag loss.

Growth measured as moult increment was defined as size (CL) at recapture minus the size at tagging or, for multiple recaptures, the size at previous recapture. The frequency distribution of moult increments was used to define measurement error and moulting. Moulting, i.e. growth, mating, and spawning, takes place between June and August or September. Recaptures from one autumn were pooled with recaptures from the following spring to obtain information from the same reproductive/growth period.

At recapture, most fishers recorded the geographical position as general locations, such as small islands or bays, so it was not possible to obtain the exact distance travelled by each recovered lobster. To overcome this problem, the Kvitsøy area was divided into small zones, according to the method described by Rowe (2001), i.e. the midpoint of a zone became the geographical position. The size of the zones typically ranged from 100 to 200 m in extension. Distance travelled was considered to be the distance from the midpoint of the release zone to the midpoint of the recovery zone. Hence, any movement within a zone could not be investigated.

The benefit of saving berried females in the fishery is the added production of eggs and larvae. The potential egg production of the landed berried females was modelled for each fishing season for the captured wild and cultured lobsters, using the commonly applied methods for calculating reproductive potential (RP), as described by Hobday and Ryan (1997) and Tully *et al.* (2001). The calculation covers the size interval from the smallest (min) to the largest (max) berried female by size

$$\underset{\mathrm{CL=min}}{\overset{\mathrm{CL=max}}{\mathrm{RP}}} = \sum (N_{\mathrm{CL}} \times P_{\mathrm{CL}} \times F_{\mathrm{CL}}).$$

Here, N_{CL} is the number of females in the landings in each size interval, i.e. those that have the potential to produce eggs, and P_{CL} is the proportion of berried females in each size interval. A logistic function was fitted to the relationship between CL and the proportion of berried females: $P_{\mathrm{CL}} = 0.34/[1 + \exp(a + b \times \mathrm{CL})]$, where $a = 27.3$ and $b = -0.34$ ($n = 10\ 600$). Data were obtained from the autumn commercial landings between 1991 and 2001 (A-LA, unpublished data). As on average 34% of the large lobsters were berried, the logistic curve was adjusted accordingly. At this point, no distinction was made between wild and cultured females. F_{CL} is the fecundity; the relationship was estimated from berried females collected at Kvitsøy (A-LA, unpublished data): $F_{\mathrm{CL}} = 0.0045\mathrm{CL}^{3.2214}$; $n = 215$, $r^2 = 0.852$.

The RP was compared with the actual egg production (AE) estimated for each spring fishing season from 1998 to 2000, because all berried females were purchased from fishers. The AE is simply expressed as

$$\underset{\mathrm{CL=min}}{\overset{\mathrm{CL=max}}{\mathrm{AE}}} = \sum (B_{\mathrm{CL}} \times F_{\mathrm{CL}}),$$

where B_{CL} is the number of berried females landed in each size interval. Females tagged in autumn and recaptured the following spring were not counted more than once, i.e. they were not included in the spring data.

Results

In all, 1204 berried females were tagged and released at Kvitsøy (Table 1), and the sizes ranged from 75 to 158 mm CL. Of these, about 34% were of cultured origin. Wild females tended to be larger than cultured females, because the cultured lobsters were not yet >135 mm CL. The proportion of berried females in the different fishing seasons varied considerably, between 19 and 58% for wild lobsters, and between 22 and 44% for cultured lobsters. A total of 312 female lobsters was recaptured at least once during the 3 y monitoring period, corresponding to an overall recapture rate of 23% (Table 2). Of these, 51 were recaptured twice, and 8 three times. Fewer cultured females were recaptured than wild females, 20 and 25% respectively (all data combined). Recapture rates varied between different release groups, females tagged and released in autumn 1998 yielding many recaptures, and females tagged and released in spring 1999 yielding few. A confounding factor is that the releases were not made as replicates. Some releases were made at sites with heavy fishing pressure, and others

Table 1. Summary statistics of berried females captured at Kvitsøy from May 1998 to May 2000, separated into wild and cultured lobsters.

Year	Season	Wild or cultured	% ovigerous	*n*	Mean CL	Minimum CL	Maximum CL	Number tagged
1998	Spring	Wild	39.0	221	105.6	75	158	119
		Cultured	41.9	64	91.8	77	127	34
1998	Autumn	Wild	46.5	257	94.7	75	157	254
		Cultured	44.2	166	91.2	77	130	153
1999	Spring	Wild	57.9	249	100.1	84	151	246
		Cultured	36.9	80	94.1	84	135	73
1999	Autumn	Wild	19.1	101	97.5	85	140	98
		Cultured	22.3	125	91.8	84	125	83
2000	Spring	Wild	56.1	113	103.8	75	154	111
		Cultured	31.0	45	92.4	85	107	33
Total				1 422	97.3	75	158	1 204

The percentage of ovigerous females sampled, tagged, and released are given. The number of animals tagged is less than sampled because some died and some cultured lobsters were used for analysis in other studies (Agnalt *et al.*, 1999).

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Table 2. Summary of recaptured females from spring 1998 to autumn 2000, separated into wild and cultured lobsters.

Tagging season	Single recaptures		% recaptured		Multiple recaptures		Total recaptures
	Wild	Cultured	Wild	Cultured	Two	Three	
1998 spring	67	5	30.3	12.8	19	5	96
1998 autumn	76	55	29.6	35.7	23	3	157
1999 spring	38	5	15.3	6.3	9		52
1999 autumn	27	9	26.7	8.7			36
2000 spring	23	7	20.9	21.2			30
Total	231	81	24.6	19.8	51	8	371

with less fishing pressure, so making a direct comparison of recapture rates difficult.

Streamer-tag loss after about 6 months in the holding facility was 3% for the two experiments (Table 3). Tagging mortality was not a factor in any of the experiments.

Growth

The frequency distribution of growth increments was used to define measurement error and to estimate average moult increment (Figure 4). The variability around zero indicates the measurement error of recaptured lobsters that had not moulted. Despite fewer observations for cultured lobsters, the pattern is identical for wild and cultured females. Growth increments of 2 mm or less were considered as measurement errors rather than growth (Conan and Gundersen, 1979; Tremblay and Eagles, 1997). Using recapture data in which time at large only included one growth season, females on average increased by 7.1 mm at each moult, independent of pre-moult size (s.d. $= 1.8$; $n = 198$; Figure 5). No significant differences in mean CL moult increment could be found between cultured and wild females (t-test; $p > 0.4$).

Reproductive cycle

In general, females had a 2 y cycle, spawning in early autumn (becoming berried) of 1 year, hatching the eggs the following summer, and then moulting (and probably mating) in late summer or early autumn (Table 4). After moulting, females were unberried for about a year until spawning again the next autumn. This process was also observed on an individual level. As much as 7–8% were berried in two consecutive years and, of these, almost half had also moulted. All but 11 of the recaptured females were $<$120 mm CL at release. Of the 11 females $>$120 mm CL at release, three (27%) were berried in two consecutive years, and one had even moulted. The remaining 9 females all followed the 2 y reproductive cycle.

Movement

Recaptures of 116 females with information on recapture site showed that as many as 40% had not moved out of their release zone (Table 5). In total, 84% remained within 500 m of the release zone, and there were no differences in movement between wild and cultured females. Only a few lobsters moved more than 1000 m. There was a tendency for females to move farther with longer time at large, but movement seemed to stabilize between 1–2 y at large.

Potential egg production of landed females

The number of eggs that would have been saved by a ban on catching berried females varied considerably among seasons, because of the annual and seasonal variation in numbers landed, in the size distribution of landed females, and in the annual variations in the ratio of females berried (Table 1, Figure 6). The largest estimate of egg production (RP) was 4.5 million eggs potentially saved in autumn 1999, of which 48% were from cultured females (Table 6). The lowest estimate of RP was in spring 2000, with only 1.4 million eggs being saved, a reduction of 70%. Actual egg production was generally higher than estimated RP for wild lobsters, with the exception of autumn 1999, when the number of berried females was extremely low compared with the average maturation ogive used in the model to estimate RP. There were small differences between AE and RP for cultured lobsters, except in spring 1999, when the ratio of berried females was very low for cultured females too. Total RP for the entire study period underestimated egg production by about 2.2 million eggs compared with actual egg production. Whereas, cultured lobsters contributed 37% of the total RP, they generated just 26% of actual egg production for the entire period. Maximum egg production is generally by lobsters above the mean sizes targeted by the fishery (Figure 6). Wild females below the minimum legal size (MLS) of 88 mm CL contributed just 3–8% of the RP. If the MLS were to be increased to 100 mm CL, 32–54% of RP would potentially be saved. Additionally, most of these lobsters would contribute to future spawning. It is important to emphasize that MLS is an important management measure when spawning biomass is well above a critical level.

Discussion

All female lobsters, independent of their pre-moult size and whether they were wild- or hatchery-reared, increased by an average of 7 mm CL at each moult. Similar growth increments

Table 3. Estimation of streamer-tag loss for berried female lobster (*H. gammarus*) held in a holding facility/lobster pound for about 6 months.

Season	Number recaptured with tag	Number recaptured having lost tag	% tag loss
First	174	5	2.8
Second	291	9	3.0

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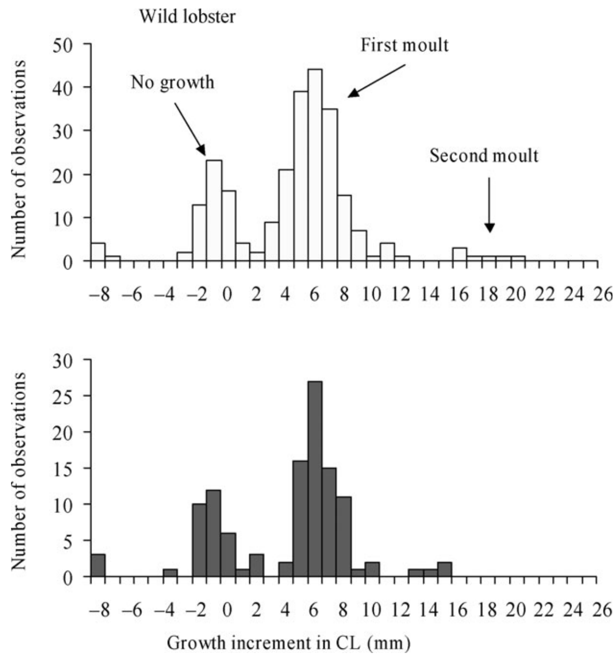

Figure 4. Frequency of growth increments in CL (i.e. difference between premoult and post-moult size). Increments of 2 mm and less were considered to be measurement error.

have been found off southern Norway by Dannevig (1936), off Ireland by Gibson (1958), and off England by Thomas (1958), Simpson (1961), Hepper (1967), and Bennett *et al.* (1978). The lack of a relationship between growth increment and pre-moult size has also been documented for female American lobsters (*H. americanus*) by Ennis (1972), Tremblay and Eagles (1997), and Comeau and Savoie (2001). However, it may vary among populations.

The pattern of a 2 y reproductive cycle (berried, moult, then berried again) is described here for European lobsters off south-western Norway. A 2 y reproductive cycle has also been documented for American lobsters off Newfoundland (Ennis, 1980, 1984), in the southern Gulf of St Lawrence (Comeau and Savoie, 2002a), in the Bay of Fundy (Campbell, 1983), and in females kept in the laboratory for 13 y (Waddy and Aiken, 1986). However, a deviation from this general pattern was reported by Latrouite *et al.* (1981) for a lobster stock in the Bay of Biscay off France, where as many as half the mature females spawn each year. Only 7–8% of the females found in this study were berried in two consecutive years, but about half of these had also moulted (so called "super-females"). In the American lobster, Campbell (1983) and Comeau and Savoie (2002a) stated that up to 20% could spawn in successive years, and Comeau and Savoie (2002a) also reported some "super-females". Those authors hypothesized that consecutive spawning without moulting mainly occurs in first-time spawners, contradicting the findings of Waddy and Aiken (1986), who suggested that the biennial spawning strategy changed in females >120 mm CL. We found that, of our 11 females >120 mm CL, only three were berried in two consecutive years (one also moulted), whereas the remaining females all followed the 2 y reproductive cycle (73%).

A biennial reproductive cycle implies that the proportion of berried females observed should approximate 50%. This was not the case in this study, and indicates a lower catchability of berried females than non-berried. Branford (1979), Krouse (1989), Miller

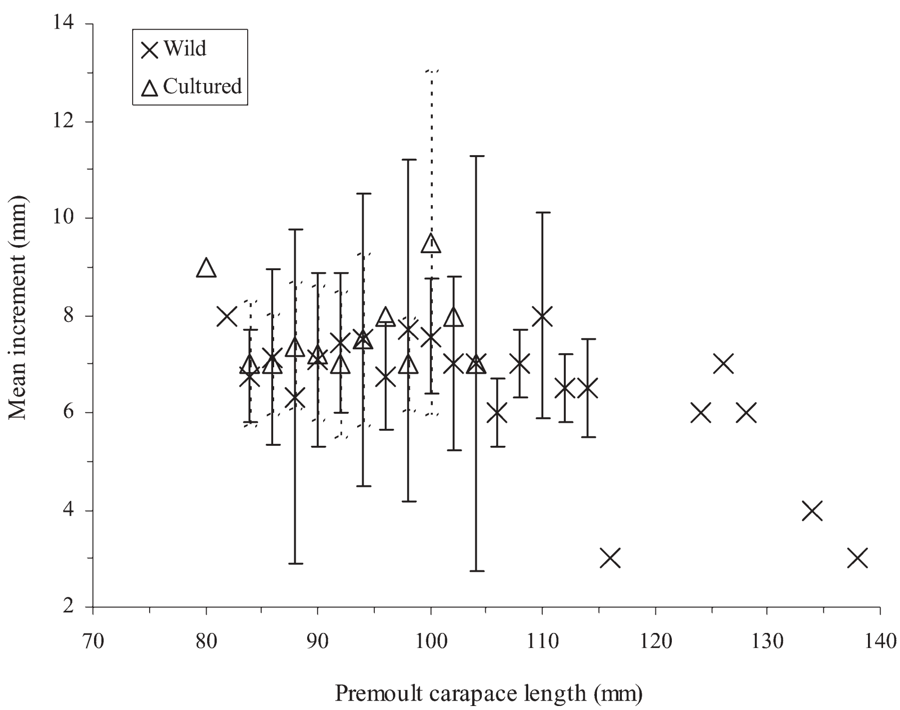

Figure 5. Mean size increment in CL (mm) after one moulting period for female lobsters; cultured females, open triangles (dotted = 1 s.d.) and wild females, crosses (solid line = 1 s.d.). Data represent only recaptures of lobster that had definitely moulted, and the period between release and recapture represented only one growth season.

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Table 4. Percentage of recaptured lobsters that moulted (M) and/or became ovigerous (O) during growth seasons between summer 1998 and summer 2000.

Growth season	Release period								
	Spring 1998			Autumn 1998 and Spring 1999			Autumn 1999 and Spring 2000		
	%M	%O	*n*	%M	%O	*n*	%M	%O	*n*
Summer 1998	87.8	8.2	49						
Summer 1999	11.1	77.8	9	92.7	7.3	110			
Summer 2000	100.0	33.3	3	0	100.0	19	97.0	7.6	66

Summer 1998 contains recaptures from autumn 1998 and spring 1999. Summer 1999 contains recaptures from autumn 1999 and spring 2000, to represent the similar reproductive season. Data include lobsters for which "time at large" means one growth season only. *n* is the total number of observations.

Table 5. Movement (%) of wild and cultured female lobsters tagged in Kvitsøy between 1998 and 2000.

Distance	All recaptures		Time at large (both wild and cultured)			
	Wild	Cultured	< ½ y	½ – 1 y	1 – 2 y	2 – 3 y
No movement	45	31	48	24	33	33
<500 m	41	53	45	48	38	33
500 – 1 000 m	10	14	6	16	19	33
>1 000 m	4	3	1	12	10	
Total recaptures	78	36	67	25	21	3

(1990), and Tremblay and Smith (2001) showed temporal changes in catchability related to sex, size, reproductive status, and season. Therefore, it is important to be aware of these factors with respect to the population studied, and the conclusions drawn.

We found that 84% of the berried females remained within 500 m of the release site. Previous studies on *H. gammarus* have also shown that most animals move distances <10 km (Appelöf, 1909; Dannevig, 1936; Simpson, 1961; Bannister *et al.*, 1994). European lobsters have in some cases moved up to 15 km from a release site, although this distance was documented in relation to the potential use of artificial reefs for stock-enhancement (Jensen *et al.*, 1994). It must be emphasized that in all of these studies, the possibility of homing has not been considered, especially when the release site differed from the catch site. Long-distance migration and homing is known in some species of spiny lobster (Herrnkind, 1980; Boles and Lohmann, 2003). Little movement has also been reported for coastal stocks of American lobster (Pezzack, 1987; Comeau *et al.*, 1998; Tremblay *et al.*, 1998; Rowe, 2001; Comeau and Savoie, 2002b), but long-distance migration has been documented for some stocks (Campbell *et al.*, 1984; Campbell and Stasko, 1985; Campbell, 1986). Pezzack and Duggan (1986) found some evidence of homing or return migration in relation to reproduction by an offshore stock. Therefore, when studying movement/migration, it is important to ensure that the recapture site and the release site are the same, to avoid homing effects.

In many mark-recapture studies, the tagging method as well as the type of tag used differed. Little is known of the effects on, for instance, growth, reproduction, and behaviour in general, although much work has focused on mortality rates (for fish, McFarlane *et al.*, 1990; for crustaceans, Cooper, 1970). Fogarty (1995) said that estimates of moulting probability and of the proportion moulting can be biased for tag loss or mortality associated with moulting. In this study, there was no mortality in the holding facility, and an estimate of streamer-tag loss of 3% is considerably less than that reported by Rowe and Haedrich (2001), but corresponds with that of lobsters tagged in post-moult condition in the southwestern Gulf of St Lawrence (Comeau and Mallet, 2003).

In this study, the tag was inserted on the ventral side of each lobster, and the needle and the tag passed through the two ventral muscles (Figure 3), whereas all the other studies used the tagging method described by Moriyasu *et al.* (1995), i.e. from the dorsal side through the dorsal muscle, diagonal to the ventral side and its corresponding muscle. The streamer tag then becomes visible both dorsally and ventrally, and visibility on the dorsal side might have attracted potential predators. Rowe and Haedrich (2001) suspected that cunner (*Tautogolabrus adspersus*) had removed some of the tags, their supposition being based on recovery of stretched and partly damaged tags, some even with small holes and teeth marks. We also found damaged streamer tags (with stretched and damaged ends) that could be attributed to interspecific interaction.

Models estimating egg production per recruit have been recommended and applied as management targets or reference points in American and European lobsters (Campbell and Robinson, 1983; Campbell, 1985; Campbell and Pezzack, 1986; Daniel *et al.*, 1989; Hobday and Ryan, 1997; Tully, 2001; Smith and Addison, 2003; Caddy, 2004; Fogarty and Gendron, 2004). We were able to compare estimates from a theoretical model (RP) with actual values (AE). In general, RP underestimated egg production by about 2.2 million eggs over the entire period. The RP model used a sigmoid maturation ogive with an asymptotic value of 0.34, based on an average over 11 y. However, for the period reported in this paper, i.e. from spring 1998 to 2000, the number of berried females was higher than average, probably caused by the warm summer and autumn of 1997 (Aure, 1997). However, both models showed a decreasing trend in egg production through time. There were considerable variations between the seasons in how many females are berried and hence producing eggs. In a lobster population off the southeast coast of Newfoundland, Ennis (1991) found similar results and showed that egg production varied from 7 to 86 million eggs over a period of 11 y. He attributed some of the difference to a variation in the percentage of berried females, which itself is related to moulting frequency. The annual variation demonstrates how indispensable time is as a factor for protecting berried females so that they may enhance long-term production. Such variability is very important to communicate to managers, to preclude them making hasty decisions when considering the effects of new regulations.

A ban on landing berried *H. gammarus* has been part of the fishery restrictions in the UK since 1951, but it was lifted in 1966 owing to enforcement difficulties and the lack of any documented positive effect (Bennett and Edwards, 1981). Also, the USA and Canada protect berried female American lobsters (*H. americanus*), and implement v-notching, i.e. marking the uropods of female lobsters (Miller, 1995). Daniel *et al.* (1989) showed that v-notched female American lobsters produced about nine times more eggs than un-notched lobsters. Tully (2001) evaluated a voluntarily v-notch programme in southeast Ireland, and showed that the annual RP from protected females was 26 million eggs. After 6 y,

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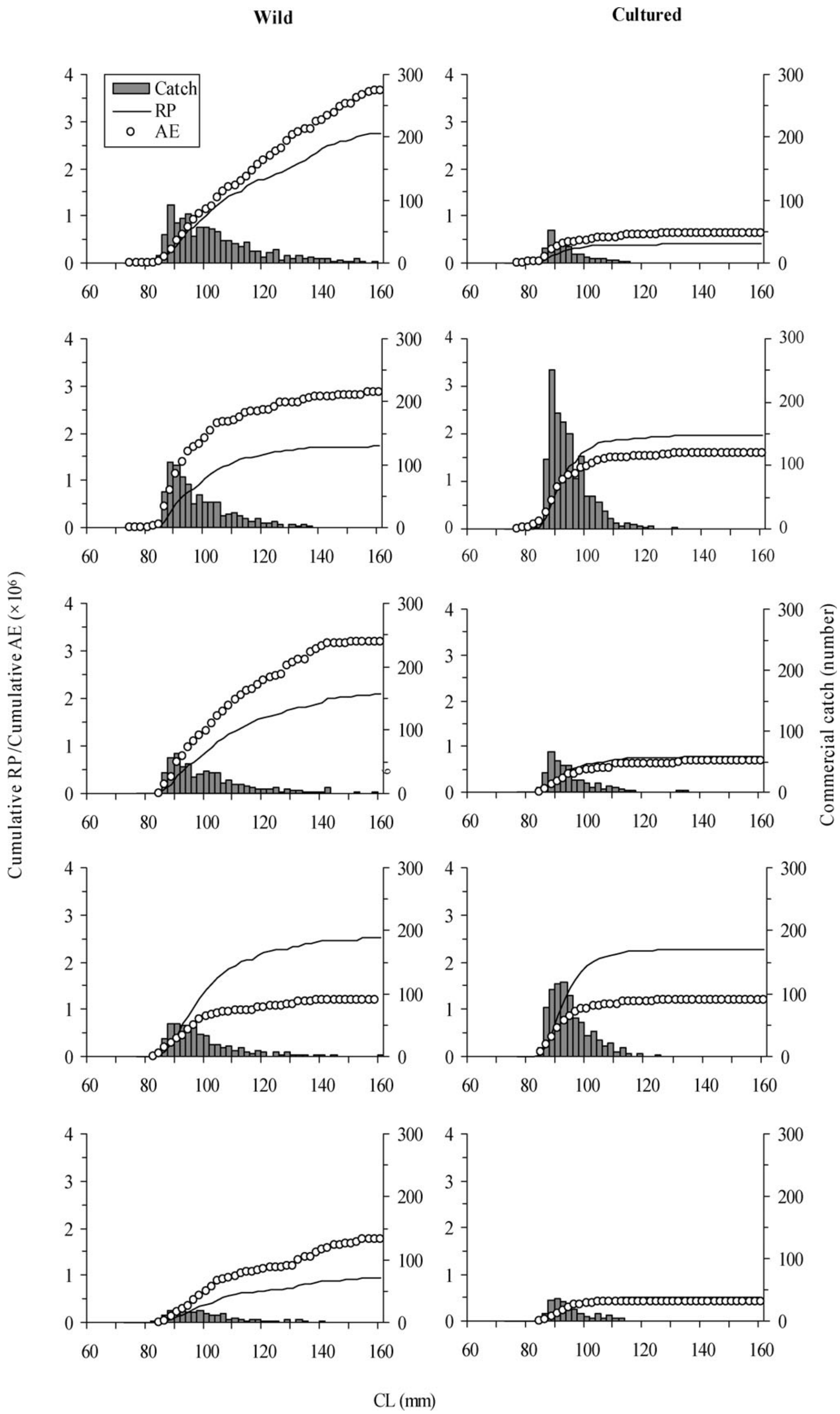

Figure 6. Estimated cumulative RP and AE for each fishing season for wild and cultured lobster combined with the length frequency distribution (females and males) in the landings.

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Table 6. Total estimated relative RP and AE for wild and cultured female lobsters.

Season	Wild		Cultured	
	RP	AE	RP	AE
Spring 1998	2 745.4	3 666.2	412.9	624.9
Autumn 1998	1 718.3	2 857.9	1 963.0	1 583.8
Spring 1999	2 096.8	3 195.3	770.8	685.8
Autumn 1999	2 506.6	1 211.5	2 263.7	1 191.2
Spring 2000	946.1	1 766.1	501.5	413.2
Total	10 013.1	12 697.0	5 911.9	4 499.0

these females contributed 59% of the total RP. The objective of protecting berried or mature females is that total egg production will increase for that population in that area. This might result in better recruitment, especially during years with favourable environmental conditions.

The consequence of a ban on landing berried females would be that females are protected from the fishery every second year, i.e. if we assume a 2 y spawning cycle. This means that fishing mortality on females would be reduced by half. However, as indicated above, the catchability of berried females seems to be less than that of unberried females, which means that the beneficial effects of a reduction in fishing mortality also will be less. If a ban should produce any effect on recruitment, the population size must be recruitment-limited, i.e. too few recruits being produced, and the main cause of mortality must be fishing. Additionally, local recruitment must originate from the areas where the ban on berried females is enforced. Poor recruitment is obviously the situation for the Norwegian stock, and the most probable reason is the huge decrease in spawning biomass. It is not known whether local recruitment originates from local areas or from more distant areas. The relatively high but variable recapture rates indicate relatively high, but area-dependent, fishing mortality. A ban should produce an immediate effect on the numbers of larvae hatched. The accumulated effect of several spawnings (long term) of the same individuals will be even more important, especially when fishing mortality is kept low. To increase the spawning stock quickly, zero fishing is obviously the best choice. Second choice would be to ban landing females, irrespective of whether or not they were berried. A total ban will of course reduce the landings to zero, whereas a prohibition on landing berried females will keep the landings at the same level because the lobsters will be larger when they are eventually captured. However, the spawning-stock biomass, potential egg production, and recruitment will increase at a slower rate.

The current MLS in western Norway of 88 mm CL ensures that virtually all females are mature. However, the contribution to egg production from small females (<88 mm) is less than 8%. Maximum egg production is by lobsters above the mean sizes targeted by the fishery, so making the current MLS less adequate as a conservation measure in terms of the reproductive potential. Increasing the MLS to 100 mm CL would save as much as 30–50% of the landed eggs for the forthcoming hatching season. In addition, many of those lobsters will contribute to egg production in future. The contribution from previously hatchery-reared and released lobsters is significant and during the studied period accounted for 26% of total egg production.

In summary, this project has shown that a ban on landing berried females is feasible to implement. The fishers believe in it and even suggested reducing their own income to help to overcome the financial limitations of the project. We are confident that such a management restriction would be welcomed by most Norwegian fishers. Although a beneficial effect on stock size has yet to be proven, there is no doubt that RP would increase substantially with such a restriction.

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References

Agnalt, A-L., Jørstad, K. E., Kristiansen, T., Nøstvold, E., Farestveit, E., Næss, H., Paulsen, O. I., *et al.* 2004. Enhancing the European lobster (*Homarus gammarus*) stock at Kvitsøy Islands; perspectives of rebuilding Norwegian stocks. *In* Stock Enhancement and Sea Ranching. Developments, Pitfalls and Opportunities, pp. 415–426. Ed. by K. M. Leber, S. Kitada, H. L. Blankenship, and T. Svåsand. Blackwell, Oxford.

Agnalt, A-L., van der Meeren, G. I., Jørstad, K. E., Næss, H., Farestveit, E., Nøstvold, E., Svåsand, T., *et al.* 1999. Stock enhancement of European lobster (*Homarus gammarus*); a large-scale experiment off south-western Norway (Kvitsøy). *In* Stock Enhancement and Sea Ranching, pp. 401–419. Ed. by B. Howell, E. Moksness, and T. Svåsand. Fishing News Books, Oxford.

Appelöf, A. 1909. Undersøkelser over hummeren (Homarus vulgaris) med særskilt hensyn til dens optræden ved Norges kyster [Investigations of lobster (*Homarus vulgaris*) with special emphasis on its behavior on the Norwegian coast]. Efter foranstaltning av Stavanger filial av selskapet for de Norske fiskeriers fremme. Bergen, A. S. Johns Griegs Boktrykkeri. 154 pp. + 10 illustrations.

J. Aure (Ed.). 1998. Havets miljø 1998 (The environmental condition in the sea—an annual report). Fisken og Havet 2: 1–90.

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 into the wild on the English east coast. Crustaceana, 67: 156–172.

Bennett, D. B., Brown, C. G., Howard, A. E., and Lovewell, S. R. J. 1978. Comparison of lobster (*Homarus gammarus*) growth rates in Norfolk and Yorkshire, England. ICES Document CM 1978/K: 6. 8 pp.

Bennett, D. B., and Edwards, E. 1981. Should we ban the berried lobsters? ICES Document CM 1981/K: 11. 11 pp.

Boles, L. C., and Lohmann, K. J. 2003. True navigation and magnetic maps in spiny lobsters. Nature, 42: 60–63.

Branford, J. R. 1979. Locomotor activity and food consumption by the lobster *Homarus gammarus*. Marine Behaviour and Physiology, 6: 13–24.

Downloaded from https://academic.oup.com/icesjms/article/64/2/288/2182156 by guest on 20 April 2024

Caddy, J. F. 2004. Current usage of fisheries indicators and reference points, and their potential application to management of fisheries for marine invertebrates. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1307–1324.

Campbell, A. 1983. Growth of tagged American lobster, *Homarus americanus*, in the Bay of Fundy. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1667–1675.

Campbell, A. 1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. North American Journal of Fishery Management, 5: 91–104.

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Canadian Journal of Fisheries and Aquatic Sciences, 43: 2197–2205.

Campbell, A., Graham, D. E., MacNichol, H. J., and Williamson, A. M. 1984. Movements of tagged lobster released on the continental shelf from Georges Bank to Baccaro Bank, 1971–73. Canadian Technical Report of Fisheries and Aquatic Sciences, 1288. 16 pp.

Campbell, A., and Pezzack, D. S. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences, 43: 2190–2196.

Campbell, A., and Robinson, D. G. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian maritimes. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1958–1967.

Campbell, A., and Stasko, A. B. 1985. Movements of tagged American lobster, *Homarus americanus*, off southwestern Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences, 42: 229–238.

Comeau, M., Landsburg, W., Lanteigne, M., Mallet, M., Mallet, P., Robichaud, G., and Savoie, F. 1998. Lobster (*Homarus americanus*) tagging project in Caraquet (1993)—tag returns from 1994 to 1997. Canadian Technical Report of Fisheries and Aquatic Sciences, 2216. 35 pp.

Comeau, M., and Mallet, M. 2003. The effect of timing of tagging on streamer-tag recapture rates for American lobster (*Homarus americanus*). Fishery Bulletin US, 101: 476–483.

Comeau, M., and Savoie, F. 2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St Lawrence. Journal of Crustacean Biology, 21: 923–936.

Comeau, M., and Savoie, F. 2002a. Maturity and reproductive cycle of the female American lobster, *Homarus americanus*, in the southern Gulf of St Lawrence, Canada. Journal of Crustacean Biology, 22: 762–774.

Comeau, M., and Savoie, F. 2002b. Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St Lawrence. Fishery Bulletin US, 100: 181–192.

Conan, G. Y., and Gundersen, K. R. 1979. Growth curve of tagged lobsters (*Homarus gammarus*) in Norwegian waters as inferred from the relative increase in size at moulting and frequency of moult. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 175: 155–166.

Cooper, R. A. 1970. Retention of marks and their effects on growth, behaviour and migrations of the American lobster, *Homarus americanus*. Transactions of the American Fisheries Society, 99: 409–417.

Daniel, P. C., Bayer, R. C., and Waltz, C. 1989. Egg production of v-notched American lobsters (*Homarus americanus*) along coastal Maine. Journal of Crustacean Biology, 9: 77–82.

Dannevig, A. 1936. Hummer og hummerkultur (Lobster and culture). Fiskeridirektoratets Skrifter, Serie HavUndersøkelser 4(12). 60 pp.

Dow, R. L. 1980. The clawed lobster fisheries. *In* The Biology and Management of Lobsters. 2. Ecology and Management, pp. 265–271. Ed. by J. S. Cobb and B. F. Phillips. Academic Press, New York.

Ennis, G. P. 1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. Journal of the Fisheries Research Board of Canada, 29: 143–148.

Ennis, G. P. 1980. Size-maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). Canadian Journal of Fisheries and Aquatic Sciences, 37: 945–956.

Ennis, G. P. 1984. Incidence of molting and spawning in the same season in female lobsters, *Homarus americanus*. Fishery Bulletin US, 82: 529–530.

Ennis, G. P. 1991. Annual variation in egg production in a Newfoundland population of the American lobster, *Homarus americanus*. *In* Crustacean Egg Production, pp. 291–299. Ed. by A. Wenner and A. Kuris. A. A. Balkema, Rotterndam. Crustacean Issues.

Fogarty, M. J. 1995. Populations, fisheries and management. *In* Biology of the Lobster *Homarus americanus*, pp. 111–137. Ed. by J. R. Factor. Academic Press, London.

Fogarty, M. J., and Gendron, L. 2004. Biological reference points for American lobster (*Homarus americanus*) populations: limits to application and the precautionary approach. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1392–1403.

Gibson, F. A. 1958. Progress Report of Ireland. ICES Document CM 1958, Shellfish Committee, 76.

Hepper, B. T. 1967. On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire. Journal of the Marine Biological Association of the UK, 47: 629–643.

Herrick, F. H. 1909. Natural history of the American lobster. Bulletin of the US Bureau of Fisheries, 29: 148–408.

Herrnkind, W. 1980. Spiny lobsters: patterns of movement. *In* The Biology and Management of Lobsters. 1. Physiology and Behaviour, pp. 349–407. Ed. by J. S. Cobb and B. F. Phillips. Academic Press, New York.

Hobday, D. K., and Ryan, T. J. 1997. Contrasting sizes at sexual maturity of southern rock lobsters (*Jasus edwardsii*) in the two Victorian fishing zones: implications for total egg production and management. Marine and Freshwater Research, 48: 1009–1014.

Jensen, A. C., Collins, K. J., Free, E., and Bannister, R. C. A. 1994. Lobster (*Homarus gammarus*) movement on an artificial reef: the potential use of artificial reef for stock enhancement. Crustaceana, 67: 198–211.

Krouse, J. S. 1989. Performance and selectivity of trap fisheries for crustaceans. *In* Marine Invertebrate Fisheries: their Assessment and Management, pp. 307–325. Ed. by J. F. Caddy. Wiley-Interscience, New York.

Latrouite, D., Leglise, M., and Taguenes, G. 1981. Données sur la reproduction et taille de premere maturité du homard *Homarus gammarus* (L.) d'Iroise et du golfe de Gascogne. ICES Document CM 1981/K: 28.

McFarlane, G. A., Wydoski, R. S., and Prince, E. D. 1990. Historical review of the development of external tags and marks. American Fishery Symposium, 7: 9–29.

Miller, R. J. 1990. Effectiveness of crab and lobster traps. Canadian Journal of Fisheries and Aquatic Sciences, 47: 1228–1251.

Miller, R. J. 1995. Fishery regulations and methods. *In* Biology of the Lobster *Homarus americanus*, pp. 89–109. Ed. by J. R. Factor Academic Press, London.

Moriyasu, M., Landsburg, W., and Conan, G. Y. 1995. Sphyrion tag shedding, and tag induced mortality of the American lobster, *Homarus americanus* H. Milne Edwards, 1837 (Decapoda, Nephropidae). Crustaceana, 68: 184–192.

Pezzack, D. S. 1987. Lobster (*Homarus americanus*) stock structure in the Gulf of Maine. ICES Document CM 1987/K: 17.

Pezzack, D. S., and Duggan, D. R. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian shelf. Canadian Journal of Fisheries and Aquatic Sciences, 43: 2206–2211.

Downloaded from https://academic.oup.com/icesjms/article/64/2/288/2182156 by guest on 20 April 2024

Rowe, S. 2001. Movement and harvesting mortality of American lobster (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1336–1346.

Rowe, S., and Haedrich, R. L. 2001. Streamer tag loss from American lobster. Transactions of the American Fisheries Society, 130: 516–518.

Simpson, A. C. 1961. A contribution to the bionomics of the lobster (*Homarus vulgaris* Edw.) on the coast of North Wales. Fishery Investigations London, Series 2, 23: 1–28.

Smith, M. T., and Addison, J. T. 2003. Methods for stock assessment of crustacean fisheries. Fisheries Research, 65: 231–256.

Thomas, H. J. 1958. Observations on the increase in size at moulting in the lobster (*Homarus vulgaris* M.-Edw.). Journal of the Marine Biological Association of the UK, 37: 603–606.

Tremblay, M. J., and Eagles, M. D. 1997. Molt timing and growth of the lobster, *Homarus americanus*, off northeastern Cape Breton island, Nova Scotia. Journal of Shellfish Research, 16: 383–394.

Tremblay, M. J., Eagles, M. D, and Black, G. A. P. 1998. Movements of the lobster, *Homarus americanus*, off northeastern Cape Breton Island, with notes on lobster catchability. Canadian Technical Report of Fisheries and Aquatic Sciences, 2220. 36 pp.

Tremblay, M. J., and Smith, S. J. 2001. Lobster (*Homarus americanus*) catchability in different habitats in late spring and early fall. Marine and Freshwater Research, 52: 1321–1331.

Tully, O. 2001. Impact of the v-notch technical conservation measure on reproductive potential in a lobster (*Homarus gammarus* L.) fishery in Ireland. Marine and Freshwater Research, 52: 1551–1557.

Tully, O., Roantree, V., and Robinson, M. 2001. Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. Journal of the Marine Biological Association of the UK, 81: 61–68.

Tveite, S. 1991. Hummerbestanden i Norge med særlig vekt på Skagerrak (Lobster stocks in Norway with special emphasize on the Skagerak area). Flødevigen Meldinger 4/1991/HFF. 12 pp.

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

Waddy, S. L., and Aiken, D. E. 1986. Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. Canadian Journal of Fisheries and Aquatic Sciences, 43: 2291–2294.

doi:10.1093/icesjms/fsl020

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