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3. Fisheries and stock enhancement

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Seksjonsleder

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Introduction

In 1995 an international group of lobster scientists as well as Norwegian students, fisheries managers and representatives from the Norwegian Council of research met at Kvitsøy for a three day long seminar to discuss the state of art in our knowledge of the European lobster *Homarus gammarus*, and the need and directions of future research. Six invited speakers from United Kingdom and USA, all specialists in their field of lobster research, held introductions in their specific topics, and were joined by additionally five lobster scientists from Ireland, New Zealand, Sweden and United Kingdom. Norwegian researchers and students involved in lobster research at the time, were also present.

The aim for the meeting was to improve the understanding of the life history and ecology of the European lobster by presenting information on this wide range of topics, and to make recommendations to further research on the factors effecting the life history and ecology of this lobster and hence the lobster fisheries.

The island community of Kvitsøy, Norway, was chosen for this meeting. Norway has the northernmost lobster stock in the world, going all the way up to the polar circle. Kvitsøy has been one of the major lobster fishing communities in this country, and the location for a large scale stock enhancement programme. Understanding the lobsters biology might be more crucial in a fringe, than in the main areas.

Why should we want to know more about the European lobster? There are several reasons:

1. Economically, the lobsters is much sought for and highly priced. In the marked place it is worth more than 250 kr / 25£ per kg. A well managed lobster population supporting a sustainable fishery will be of high economic value.
2. Socio-economically, the lobster fisheries have traditionally been an important inshore fishery, supporting small communities along the coast of southern Norway.
3. The recent decline in Norwegian lobsters landings has revealed a considerable lack of understanding of lobster ecology, biology and, in particular, factor effecting recruitment to the fisheries. Adult lobsters, being top predators beside being scavengers, may play a key role in it's ecosystem. Better knowledge about the lobsters ecology might give us more knowledge of the whole ecosystem.

The meeting was based on six review presentations giving up-to-date knowledge of lobster biology and ecology from the beginning of life until fully grown, as well as lobster fisheries and cultivation. Together with the Norwegian presentations on on-going research in connection with the PUSH-programme, a base-line was drawn from which some of the most critical gaps in our knowledge could be addressed, and suggestions made for the development of more effective long-term management strategies, based on identified and well designed research projects.

This proceedings presents the six review articles, two reviews presenting Norwegian lobster fishery, management and enhancement projects and some notes from the discussions. Finally a summary presents the recommendations from the meeting on important topics to work on in the future, and a epilogue presenting the development in Norwegian lobster research since 1995. The articles are mainly based on the oral presentations, but lobster stock enhacement in the UK was presented by a video, which is summarised in this proceeding.

Overall summary

In 1995 an international group of lobster scientists as well as Norwegian students, fisheries managers and representatives from the Norwegian Council of research met at Kvitsøy to discuss the state-of-art in our knowledge of the European lobster *Homarus gammarus*, and the need and directions of future research. Invited speakers from United Kingdom and USA held review presentations on their specific topics, giving up-to-date information on: Reproduction; Larval and juvenile ecology; Habitat and Migration; Age and Growth; Stocks and Population Dynamics; and Aquaculture.

The aim for the meeting was to improve the understanding of the life history and ecology of the European lobster by presenting information on this wide range of topics, and to make recommendations to further research on the factors effecting the life history and ecology of the European lobster and hence the lobster fisheries.

The reviews and the Norwegian presentations on on-going research made together a base-line from which some of the most critical gaps in our knowledge were addressed. Suggestions were made for the development of more effective long-term management strategies, based on identified and well designed research projects. The need of reconciliation of laboratory experiences, particularly for larvae and juveniles, was an issue often raised, as well as the need to unravel the 'bottlenecks' to survival of the various life history stages, and to understand better density-dependent survival. Both aquaculture and fishery should benefit from better modelling of the variability in: Size at onset of breeding; Egg viability, Growth and survival at the various life history stages, using sensitive and standardised analyses.

Key words: Lobster; Life history; Ecology; Fisheries and assessment; Stock enhancement

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We thank the Kvitsøy Maritime for excellent service, food and accommodation. We are also grateful to all our participants for excellent presentations and keen interest in the discussions. Dr. John Dooth, NIWA, New Zealand was kindly rapporting during the seminar and ms. Helene Pedersen made an invaluable contribution as secretary. A special thanks to those who co-operated, gave advice and was involved in some way in preparing this report. Mr. Hugh Allen (Allan Market Communication) was helpful with corrections of the spelling and grammar in the final manuscript.

Sammendrag

Seminaret ble arrangert for å samle sentrale forskere involvert i forskning på Europeisk hummer *Homarus gammarus*. Et bredt aspekt av hummerens biologi og forvaltning ble diskutert, inkludert hummerfiskerier, kultur og utsetting. Norge og det norske hummerfiske var i fokus, men forskerne fra Sverige, Storbritannia, Irland, USA og New Zealand var med og utdypet diskusjonene.

Seks sesjoner ble holdt, som dekket områdene reproduksjons-, larve- og yngeløkologi, habitat og vandring, alder og vekst, bestander og bestandsutvikling og kultiveringstiltak. Hver sesjon ble innledet med en grundig gjennomgang av dagens kunnskap om temaet, holdt av en ledende internasjonal forsker innen fagområdet. Denne innledningen ble fulgt opp av en kortere presentasjon av norsk kunnskap og forskningsaktiviteter innen dette området. Deretter fulgte en åpen og generell diskusjon, der også norske forhold ble satt opp mot forhold ellers i hummerens utbredelsesområde. Gjennomgangsforedragene og sammendrag av de norske innleggende er inkludert i denne rapporten, sammen med en kort oppsummering av diskusjonen i hver sesjon.

De norske undersøkelsene av hummer har inntil nå ikke vært omfattende som i USA og Storbritannia, men det ble presentert lovende framskritt innen mange områder. Seminaret bidro til å peke på og sette opp prioritering for viktige forskningsområder framover. Disse anbefalingene er tatt med i diskusjonssammendragene etter hver sesjon, men noen helt sentrale områder må nevnes spesielt, da de stadig ble trukket fram.

Det må utvikles standardmetoder for å måle variasjoner innen viktige aspekter innen hummerbiologi. Størrelse ved kjønnsmodning, eggkvalitet i form av livskraften til larvene etter klekking, vekst og overlevelse gjennom ulike livsfaser var tema som stadig kom opp. Modellering basert på standardisert datainnsamling, med analyse av betydningen av de enkelte variablene, burde lede til resultater som ville være nyttige både for kultiveringsarbeide, studier og forvaltning av det ordinære fisket.

I Norge er hummer i fangenskap mye nærmere studert enn hummer i naturen. At kunnskap fra laboratoriet, særlig om oppdrettet hummerlarver og yngel, må kontrolleres mot hva som skjer i naturen, ble det lagt stor vekt på. Også behovet for å finne fram til "flaskehalser" for overlevelse i ulike livsfaser, og å se på overlevelsen i sammenheng med individtetthett ble trukket fram. Dette er informasjon som er av stor betydning, både for forvaltning av det ordinære fiskeriet såvel som for utsettingsforetak. Vanntemperatur ble framhevet som en kritisk faktor, både for fisket, for naturlig rekruttering og for oppdrett, da temperatur har en stor innvirkning på alle livsfaser, og siden Norge ligger helt i nordlige utkanten av hummerens utbredelsesområde.

Seminaret resulterte i sentrale retningslinjer og prioriteringer for videre hummerforskning i Norge. Alle deltakerne, såvel norske som utenlandske, vil i tillegg ha nytte og glede av den gode utvekslingen av informasjon og ideer.

Reproduction in the European Lobster (*Homarus gammarus* (L.))

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Introduction

Studies of the reproductive biology of the European lobster *Homarus gammarus* (L.) are important for understanding lobster behaviour and population dynamics, and for estimating parameters such as size at maturity and fecundity at size. These are key components of stock assessment and fisheries management programmes.

A wealth of information on the reproductive biology of the American lobster (*Homarus americanus*) is available, but very little work has been done on its sibling species *H. gammarus*. Background information on *H. americanus* has therefore been used to structure this review of what is known about the reproductive biology of *H. gammarus*, and of the further studies that are required.

Size at onset of maturity

Introduction

Knowledge of the size at which sexual maturity occurs in *H. gammarus* is important in the assessment of the minimum landing size for use in management legislation. Stock reproductive potential will be affected by fishing if size at onset of maturity is close to the minimum legal landing size (Heydorn, 1964). Templeman (1939) suggested that individuals should be allowed to reproduce at least once before being removed by fishing. Coupled with fecundity estimates, size at onset of maturity may be used to model the egg production potential of stocks subjected to varying levels of fishing pressure and management legislation policies (Ennis, 1984). The accurate determination of size at maturity is additionally important because of the change in moult frequency (and therefore growth rate) that occurs after females become sexually mature (Simpson, 1961). The onset of maturity may also be accompanied by changes in lobster behaviour and potential changes in the nature and degree of local movements or migration in *Homarus spp.*(Cooper and Uzmann, 1980; Campbell, 1986).

Physiological vs. functional maturity

In male lobsters two distinct aspects of sexual maturity have been identified (Aiken and Waddy, 1980), as well as in other decapod crustaceans (e.g. *Chionoecetes opilio*, Conan and Comeau, 1986). The onset of physiological maturity occurs when the male becomes capable of producing mature spermatozoa, but it is not until the male is also functionally mature that it is capable of mating with, and successfully inseminating a female.

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The onset of physiological maturity may be determined by the presence of spermatozoa in the vas deferens, identified by histological methods. The size at onset of physiological maturity in male *H. americanus* was investigated by Krouse (1973) and found to be as small as 40-45 mm carapace length (CL). Briggs and Muschake (1979) found all but one male with sperm in its testes and/or vas deferens when examining *H. americanus* males as small as 57mm CL (much below the observed size of female maturity). Free (1994) did not observe any male *H. gammarus* without sperm in its testes, although the smallest size examined was 73mm CL, and smaller individual males would be required to assess the onset of physiological maturity.

Templeman (1934) conducted mating experiments on *H. americanus* and found that males of less than 65 mm CL were too small to mate with sexually mature females, although Hughes and Matthiessen (1962) suggested that small males do try to mate with females much larger than themselves, with variable success. Male *Jasus spp.* apparently become functionally mature at similar sizes to females, and occasionally at a slightly smaller size (Heydorn, 1965; MacDiarmid, 1989).

Female *Homarus spp.* are considered to be functionally mature when capable of mating and egg extrusion. Differences in size at physiological maturity and functional maturity may be most easily determined using ovary morphology and the presence of eggs as respective indicators. The determination of functional maturity using internal condition indices may be complicated by the earlier onset of physiological maturity (MacDiarmid, 1989). Expressed maturity (i.e. carrying eggs) may also be considered for *Homarus spp.* females, because the reproductive cycle is not annual (Aiken and Waddy, 1980). Ennis (1980) described expressed maturity as being more important than physiological female maturity for management considerations as only those females which produce eggs in any given year will contribute to that year's egg production. This is confused by potential changes in catchability during the reproductive cycle (Hallbäck and Warren, 1972; Branford, 1977), and by difficulties in determining whether a lobster will become berried in the course of a given year.

Male size at maturity

The validity of external male maturity indicators for *H. gammarus*, using cheliped propodite dimensions, is of considerable importance for fisheries management. The success of fisheries management based upon minimum legal landing size legislation (MLS), undoubtedly relies on MLS being above the size at functional maturity of an adequate proportion of individuals in order to avoid recruitment failure. The difference, however, between size at onset of male lobster maturity and MLS may not be as critical as female maturity from a management perspective, assuming that some lobsters will always avoid capture and the potential for multiple insemination by individual males.

Determination of male size at onset of maturity

Since the presence of spermatozoa in the vas deferens of male homarid lobsters is not a valid indication of functional maturity (Van Engel, 1980; Aiken and Waddy, 1980), and it is impractical to assess the size at which the ability to mate develops, other methods have been devised for use in the field.

Internal indices of maturity

Aiken and Waddy, (1980) observed a relationship between vas deferens weight and the onset of functional sexual maturity in *H. americanus* and developed a vas deferens factor (VDF) (Table 1) to exploit this. They suggested that there is a uniform size of vas deferens at maturity in *H. americanus,* irrespective of male size, thereby reinforcing the potential use of vas deferens weight, in some format, for estimating male size at onset of maturity. MacDiarmid (1989) demonstrated highly variable vas deferens wet weights in male *J. edwardsii* of a given size and suggested that the males must have been caught at various intervals after mating, thereby implying the requirement of a recovery time before males could successfully fertilise eggs again. This is also suggested by Aiken and Waddy (1991) for *H. americanus,* with lobsters exhibiting considerable variation in potency and enthusiasm to re-mate, both within and between individuals. Free (1994) used the VDF in order to assess maturity in male *H. gammarus*, but this did not show any distinct inflection points when plotted against CL; VDF also showed a high degree of individual variability (Figure 1). However, the vas deferens weight plotted against CL did produce an inflection point that may be considered as an indication of size at onset of maturity (Free, 1994), with an increase in individual variation after the inferred size at onset of maturity, suggesting variability in recovery time after mating as suggested by MacDiarmid (1989) and Aiken and Waddy (1991).

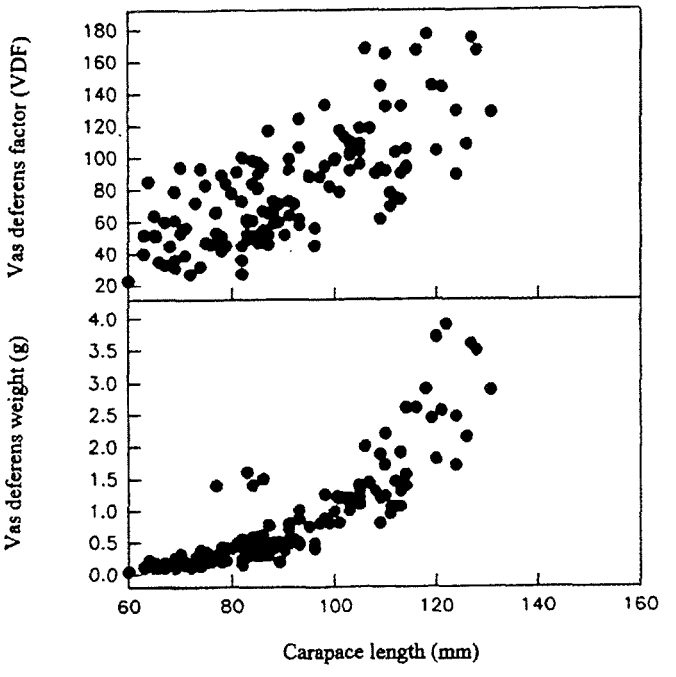

Figure 1 Internal metods for determining the size of maturity of male *H. gammarus* (data collected in Yorkshire, 1981)

Figur 1 Metode for innvendig analyse av kjønnsmodning relatert til størrelse av hann-hummer. (Data samlet i Yorkshire, 1981)

External indicators of maturity

Templeman (1935) observed changes in the size of the crusher chelipeds of male *H. americanus* relative to total body length, after functional maturity and suggested the use of cheliped propodite length as an indicator of sexual maturity (Table 1). Aiken and Waddy (1980) suggested that this method was invalid as an indicator of male functional maturity in *H. americanus* when CL was used instead of total length; and that cheliped propodite length directly plotted against CL (CPL) (Table 1) did not indicate a clear inflection point for the onset of maturity (c.f. Free, 1994 for *H. gammarus*, Figure 2).

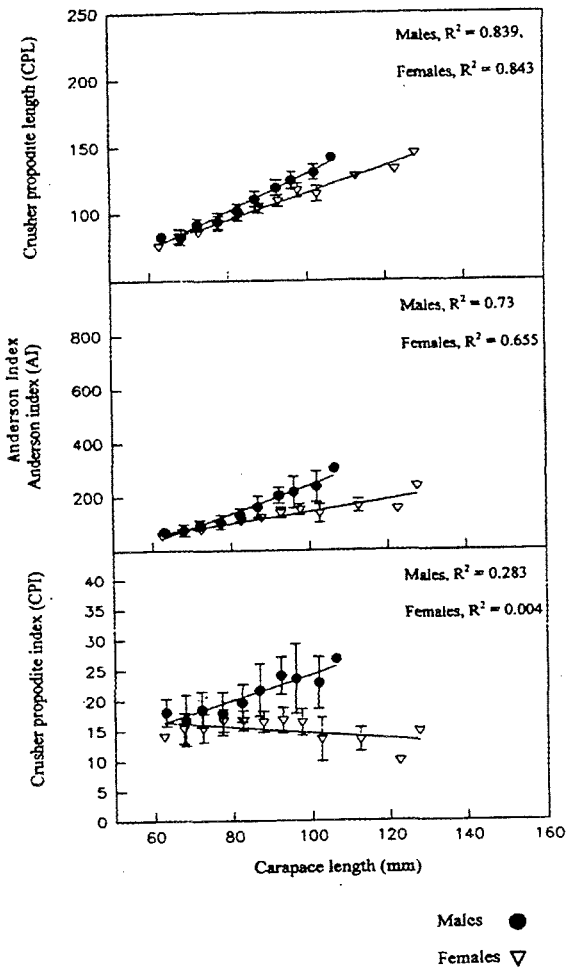

Figure 2 External methods for determining the size at onset of maturity of male *H. gammarus*, with linear model regression lines (data in 5 mm groups; collected in Yorkshire 1989).

Figur 2 *Ytre mål for analyse av kjønnsmodning i forhold til størrelse hos hannhummer. (data in 5 mm groups; samlet i Yorkshire 1989).*

Squires (1970) and Ennis (1971; 1980) observed a strong inflection at maturity caused by the positive allometric increment of crusher claw weight when compared against carapace length, but this method has not been widely used because it is impractical to use in the field. Aiken and Waddy (1980) devised the "Anderson cheliped index" (AI) (Table 1) to take crusher claw volume into account without having to measure claw weight. The Anderson index, plotted against CL, appears to exhibit an inflection for male lobsters which may be regarded as representing male functional maturity (Aiken and Waddy, 1980). The use of the Anderson index was disputed for *H. americanus* by Ennis (1980), who did not observe such an inflection point. In *H. gammarus* the inflection point is not always easily determined and the difficulty in its accurate calculation prohibits the use of the AI (Free, 1994) (Figure 2).

Table 1 Male maturity indices
Tabell 1 Kjønnsmodningsindex for hanner

Indicator	Author	Calculation
Vas deferens factor, (VDF)	Aiken and Waddy (1980)	VDF = [(Vas deferens wet weight, mg)/CL^3(mm)] x 100 Plot against CL (mm)
Cheliped propodite length vs total length	Templeman (1935)	CPL = Crusher propodite length (mm) Plot against TL (mm)
Cheliped propodite length vs CL (CPL)	Aiken and Waddy (1980)	CPL = Crusher propodite length (mm) Plot against CL (mm)
Anderson index (AI)	Aiken and Waddy (1980)	AI = [CPL x width x depth (mm)]/ [CL (mm)x10] Plot against CL (mm)
Cheliped propodite index (CPI)	Aiken and Waddy (1989b)	CPI = [CPLx width x depth (mm)x 100]/ CL^3(mm) Plot against CL (mm)

Aiken and Waddy (1989) developed an alternative method, using the crusher cheliped propodite index (CPI) (Table 1), which gives a distinct point of inflection at the size at onset of functional maturity. The CPI, when plotted against CL intersected the female regression line of CPI at the point of male functional maturity for *H. americanus* (Aiken and Waddy, 1989b). In contrast, Free (1994) did not observe a clear intersection using CPI for *H. gammarus* because of high variation about the regression lines (Figure 2).

The methods of calculating both AI and CPI involve the use of the independent variable (CL), and are therefore not as statistically valid as CPL. Furthermore, Free (1994) observed that male and female CPL vs. CL regression lines have a high correlation coefficient, in contrast to AI or CPI when plotted against CL (Figure 2). Free (1994) suggested that male/female regression line intersections on plots of CPL against CL could be used for regional and temporal comparisons of size at onset of maturity in *H. gammarus* but require further validation in relation to actual size at functional and physiological maturity.

Conan *et al.*, (1985) refuted the idea of determinate the onset of maturity of male *H. americanus* by the means of using claw morphometry (after attempting the process using log-linear transformations, bivariate allometric plots and principal components analysis), and suggested that the sexual differentiation of claw size is initiated from early juvenile stages. However, principal components analysis has since been successfully used to ascertain size at functional maturity in both *Chionoecetes opilio* (Conan and Comeau, 1986) and *Necora puber* (Freire and Gonzalez-Guirriaran, 1992).

Female size at maturity

Ovary development

As with those of other decapods, the ovaries of *H. americanus* and *H. gammarus* go through changes in colour and size during their development to maturity. In *Homarus spp.* ovarian maturation becomes macroscopically evident when ovoverdin carotenoprotein appears in the yolk mass, thus giving the ovarian tissue a green colour (Aiken and Waddy, 1980). Once maturity has been reached, similar changes in colour and size occur during succeeding reproductive cycles. Six arbitrary developmental stages (including the spent or reabsorbing state) have been assigned to the ovary of *H. americanus* according to oocyte size, and ovary size and colour, by Aiken and Waddy (1980) and for *H. gammarus* by Free (1994) (Table 2).

Table 2 Ovary development stages of H. gammarus (Free, 1994)
Tabell 2 Utviklingsstadier av ovarier hos H. gammarus (Free, 1994)

Ovary stage	Description	Ovary Colour	Oocyte Diameter (mm)
1	Immature	White	<0.5
2	Immature	Yellow, beige or pale green	<0.8
3	Immature/ Developing	Light to medium green	<1.2
4	Developing	Medium to dark green	0.5 to 1.4
5	Developing	Dark green	0.8 to 1.7
6	Developing	Dark green	1.2 to 1.7
6a	Ripe		
Spent/ Reabsorbing	Oocytes free	White/yellow with residual ova	

The ovarian cycle

After sexual maturity, the growth of oocytes to maturation and ovulation results in growth and regression of the ovary, i.e. the ovarian cycle. In *H. americanus* and *H. gammarus* the ovarian cycle may take two years to complete (Aiken and Waddy, 1980), although the population breeds annually. The length of time of the reproductive cycle is influenced by size, most probably a result of essential interactions with the moult cycle (Adiyodi and Adiyodi, 1970), and resource allocation between somatic and reproductive growth. Female lobsters usually mate only when their exoskeleton is soft, just after ecdysis, although some evidence exists of inter-moult mating (Aiken and Waddy, 1980; Dunham and Skinner-Jacobs, 1978).

The timing of both moult and egg extrusion has been shown to vary throughout the lifespan of the female *H. americanus* (Aiken and Waddy, 1976) with larger females extruding eggs later in the season. This may be a response aimed at optimising energy partitioning at different stages of an individual's life history (Attard and Hudon, 1987). Larger female American lobsters in the Iles de la Madeleine (Quebec) were shown to carry more developed eggs than smaller individuals (Attard and Hudon, 1987) and this phenomenon may be related to differing times of egg extrusion and/or local temperature regimes during egg development.

Variation in spawning season

Geographical variation in the precise timing and seasonal occurrence of moult and reproductive cycle events may occur in both *H. gammarus* and *H. americanus* populations. This suggests a potential variation in spawning times between areas with differing temperature regimes. Templeman (1940) was the first to noticed a marked difference in the spawning times of *H. americanus* from different localities with varying average sea temperatures. In the UK, the main spawning period of *H. gammarus* populations has been reported to begin in July and finish in September (Branford, 1978), although spawning in June is not uncommon (Free, 1994). *H. americanus* females have been reported to spawn at any time between May and October, but most commonly between June and September (Herrick, 1894; Templeman, 1940; McLeese and Wilder, 1964; Thomas, 1973; Aiken and Waddy, 1980). Temperature is believed to regulate spawning, with lobsters from warmer waters starting egg incubation later than individuals from cool-water areas (Templeman, 1940; Aiken and Waddy, 1990). In the absence of temperature variation, maturation, vitellogenesis and spawning require photoperiod cues as exogenous controls (Aiken and Waddy, 1990). The frequency of spawning may also vary with temperature; Ennis (1971) discovered that *H. americanus* from relatively cold Newfoundland waters might only spawn every fourth or fifth year.

Sastry (1983) reviewed other possible influences on gametogenesis and other aspects of the crustacean reproductive cycle. These factors include photoperiod, food availability and social conditions (including parasitism). Oocyte growth in *H. americanus* may be arrested by dietary deficiencies in lipid or protein which may result in oocyte resorption (Aiken and Waddy, 1980; 1986). Similarly, Beyers and Goosen (1987), working on the palinurid lobster *Jasus lalandii,* showed that food availability (and quality) in the environment was a potential limiting factor on oogenesis. Gamete production may not occur at all unless a minimal amount of nutrients is available to the gonads, either directly from the environment or from a nutrient store.

Knowledge of ovarian development in *H. gammarus,* and the duration and seasonality of the cycle, are important for the validation of external functional maturity indicators. The duration of the ovarian cycle and spawning frequency affect individual fecundity, with respect to both the number of egg clutches produced and potentially, the size of egg clutches produced (as an egg clutch produced in a second consecutive year may not be as large as the initial clutch size because of inadequate resources or limited sperm availability). The length of time requrred for ovary development may therefore affect the reproductive potential of the stock.

Determination of female size at onset of maturity

Assessment of female sexual maturity in *H. gammarus* is complex because of the length of the reproductive cycle, potential variability in the duration of the cycle with female size and geographic location, and behavioural changes during the cycle (with resultant changes in female catchability).

The size at which maturity first occurs in a given lobster population may be determined by the smallest size at which ovigerous females occur (because egg-bearing females are obviously mature) (Aiken and Waddy, 1980). However, since not all females capable of egg extrusion will be berried at any given time, because of the complex, size-dependent timing of the reproductive cycle (Aiken and Waddy, 1980), examination of other internal and external morphological features may be required to determine maturity. The size-frequency distribution of both berried females and females deemed mature using other criteria may be used to calculate the size at first maturity, 50% maturity and 100% maturity.

Internal indicators of maturity

A number of internal indices have been developed to describe female reproductive condition. Gonado-somatic indices (e.g. relative ovary weight, ROW) show a significant increase as maturation approaches, with an obvious drop after spawning (Harrison, 1990; Free, 1994) (Table 3) (Figure 3). Kamiguichi (1971) suggested a proportional relationship between ovary weight and the cube of body length for the shrimp *Palaemon.* Aiken and Waddy (1980) developed this "ovary factor" (OVF) for use in *H. americanus* and found it to be effective for ovary maturity stage determination when used in conjunction with gross morphological characteristics (i.e. oocyte size and colour) (Table 3). Free (1994) suggested that OVF could be used in the determination of size at onset of maturity in *H. gammarus*, but that the increase in variability of OVF with increasing size implies preferential use of ovary development stages for maturity assessment (Figure 3).

Table 3 Female maturity indices

Tabell 3 Kjønnsmodningsindex for hunnhummer

Indicator	Author	Calculation
Relative ovary weight (ROW)	Giese (1966)	ROW = [Ovary weight (g)/Total wet weight (g)] x100 Plot against CL (mm)
Ovary factor (Ovf)	Aiken and Waddy (1980) after Kamiguichi (1971)	Ovf = [Ovary weight (mg)/CL^3 (mm)] x 10 Plot against CL (mm)
Abdomen width (AW)	Templeman (1935)	AW = Width of second abdominal segment (mm) Plot against CL (mm)
Relative abdomen width (RAW)	Templeman (1944)	RAW = [AW (mm)]/[CL (mm) Plot against CL (mm)

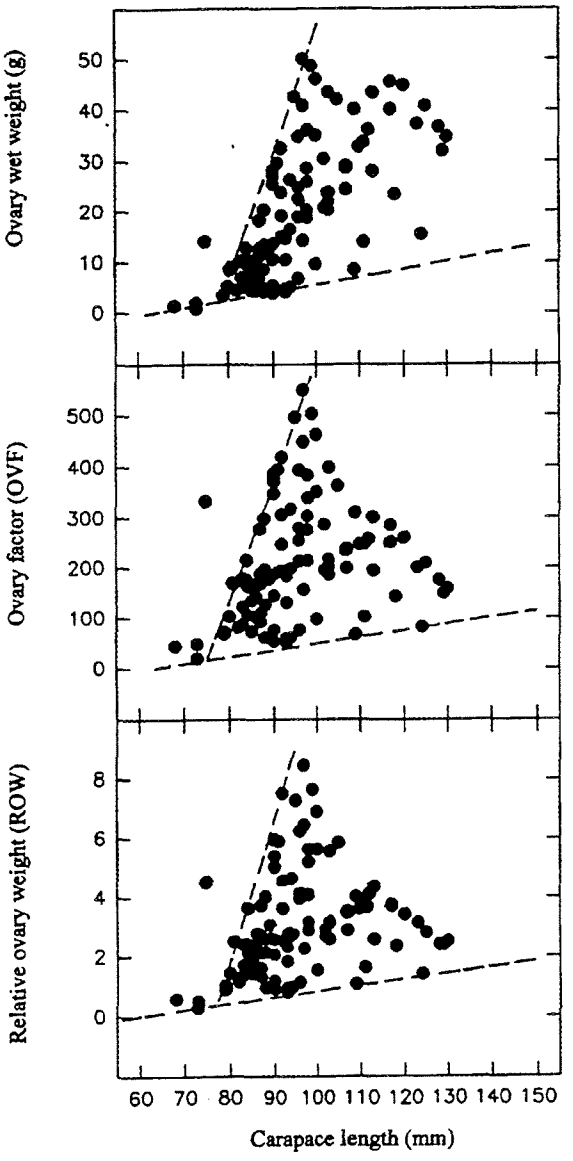

Figure 3 Internal methods for determining the size of maturity of female *H. gammarus* (data collected in Yorkshire, 1989 to 1991)

Figur 3 Metode for innvendig analyse av kjønnsmodning relatert til størrelse av hunn-hummer. (Data samlet i Yorkshire, 1989-1991)

Ovary development stage is a reliable, but unfortunately destructive method, of determining physiological sexual maturity (Figure 4). Individuals which have undergone secondary vitellogenesis, with dark green oocytes larger than 1.0 med mer diameter (ovary stage 4, 5 or 6) have been considered potentially mature (Squires, 1970) (c.f. Krouse, 1973 and Briggs and Mushacke, 1979, who suggested that oocytes> 0.8 mm diameter indicate maturity). Aiken and Waddy (1980) suggest that fully mature, preovigerous ovaries contain ova that are larger than 1.4 mm in diameter and which are free in the ovary (ovary stage 5 or 6). The ovary factor may also assist in maturity assessments as the determinate between ovary stages 4 or 5.

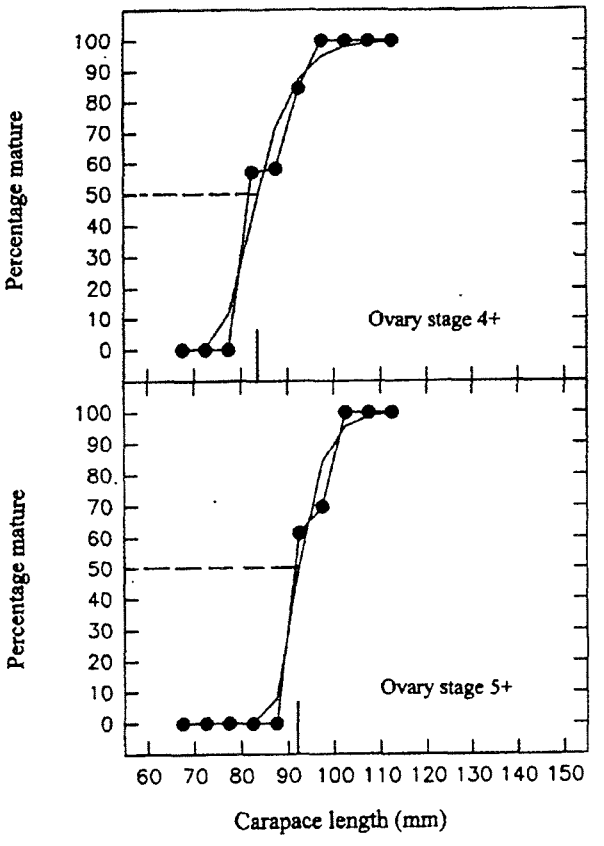

Figure 4 The use of ovary development for determining the size at onset of maturity of female *H. gammarus* with fitted logistic curves (data in 5 mm groups; data collected in Yorkshire, 1989).

Figur 4 Bruk av ovarieutvikling for å finne størrelsen ved begynnende kjønsmodning hos hunnhummer. Logistiske kurver er tilpasset dataene. (data i 5 mm grupper; data samlet i Yorkshire, 1989)

External indicators of maturity

The relative growth of secondary sexual characters has been widely used as an indication of sexual maturity in crustacean populations (Hartnoll, 1978). Templeman (1935; 1939) observed a relative increase in the width of the second abdominal segment of *H. americanus* with the approach of the onset of sexual maturity, in order to provide a larger area underneath the abdomen for protection of the eggs during incubation. Later, Templeman (1944) suggested that the relationship between abdomen width (AW) and total length could be used to facilitate comparisons between the sizes at sexual maturity of lobster populations at different locations. AW increases with CL, but less rapidly in males than females. When expressed as a percentage of the carapace length, the measure of abdominal width has been used as a maturity index, relative abdomen width (RAW), as shown by Simpson (1961), working on *H. gammarus*. Originally, the maximum inside width of the second abdominal segment was measured for use in such studies. Ennis (1971) used the maximum outside width of the segment to estimate the maturity index. This method is now preferred for its ease of use, and to increase the accuracy of the measurement, especially in field work (Aiken and

Waddy, 1980). Perkins and Skud (1969), plotting the width of the second abdominal segment of *H. americanus* against CL, revealed an inflection that corresponded to the segment width of the smallest ovigerous female. The equation describing the relationship between these two variables was cubic, with an asymptote at a female size at which most individuals might be presumed to be mature (i.e. 100 % maturity). Krouse (1973) studied the abdomen width-carapace length relationship for females of a wide size range and indicated an initial acceleration in abdomen width relative to CL in females of 30-35 mm CL, as well as a further rapid change in relative growth at maturity. In general, it has been suggested that there is a good agreement between the size at which the graphical inflection of RAW and carapace length occurs, and the smallest ovigerous females (Skud and Perkins, 1969; Krouse, 1973; Aiken and Waddy, 1980). However, Squires (1970) noticed the presence of ovigerous H. *americanus* females that were smaller than the size at maturity suggested, for the population as a whole, by the relative abdomen width index. Ennis (1980) pointed out that although a distinct inflection and then asymptote may occur when RAW is plotted against CL, the corresponding sizes at which these events occur should only be regarded as approximations of the size at onset of maturity and 100% maturity respectively within the population concerned.

The use of external indicators of maturity which use the allometric growth of the second abdominal segment, requires physiological validation. Work on the relative abdomen width of *H. americanus* has revealed a strong correlation between oocyte size and the width of the second abdominal segment (Skud and Perkins, 1969). Free (1994) suggests that in *H. gammarus*, the widening of the abdomen begins before size at functional maturity (possibly two moults), and also before commencement of ovary development (onset of physiological maturity) (possibly one moult). Estimates of physiological maturity using ovary staging are unfortunately destructive, and do not allow for observation of the interval before onset of functional maturity. The use of relative abdomen width as an indicator of maturity in *H. gammarus* is dubious because of the lack of correlation between male RAW and CL (for intersect analysis) (Figure 5), and statistical difficulties in the determination of any suggested inflection which might infer functional or physiological maturation for any given population (Free, 1994). Variability in individual growth rates and individual relative growth is not adequately compensated for by size class grouping of individuals for inflection identification; this may also be problematic for intersect analysis. Between-year differences in AW-CL relationships cannot be adequately explained and may also invalidate the use of AW-CL and RAW indices for identifying size at onset of maturity in *H. gammarus* (Free, 1994).

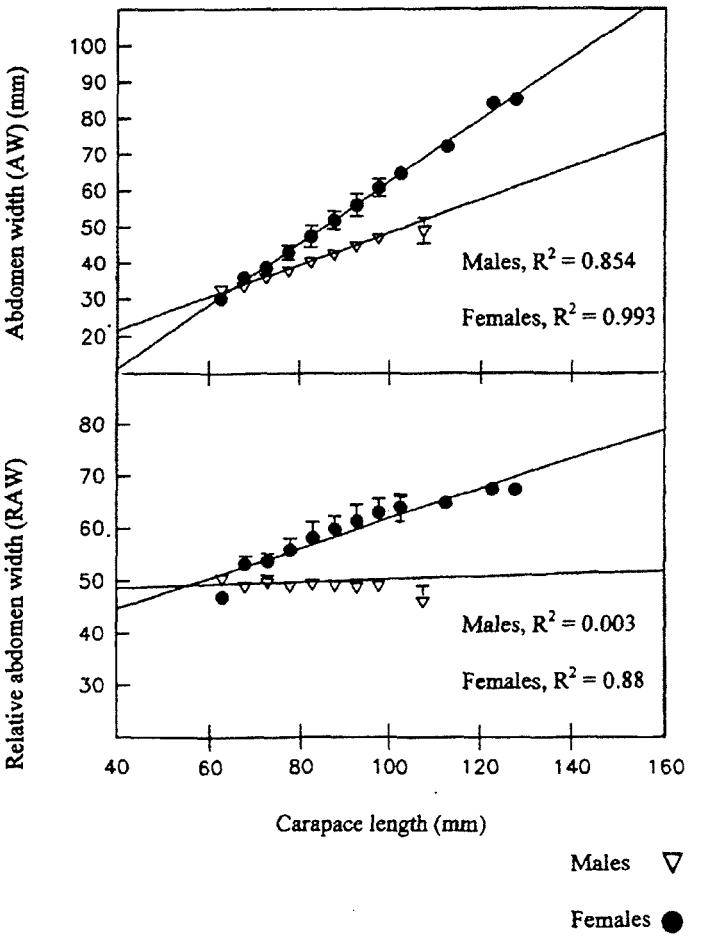

Figure 5 External methods for determining the size at onset of maturity of female *H. gammarus*, with linear model regression lines (data in 5 mm groups; collected in Yorkshire 1989)

Figur 5 Ytre mål for å finne størrelsen for begynnende kjønnsmodning av hunnhummer. Modellerte lineære regresjonslinjer er vist i figuren. (data i 5 mm grupper; samlet i Yorkshire 1989)

Evidence of the presence of FSP (female specific hormone) may be used as an external maturity indicator. FSP is immunologically identical to the major yolk protein present in the haemolymph of female *Homarus spp.* during yolk mobilisation associated with massive oocyte resorption and secondary vitellogenesis (Barlow and Ridgway, 1969; Byard, 1975). Haemolymph containing FSP is a distinctive dark green colour, which may be observed externally through the ventral abdominal membrane, thus indicating the maturity of the individual concerned (Aiken and Waddy, 1980). Free (1994) suggested that females exhibiting a dark green abdomen had ovaries at stages 5 or 6 but that the majority of female *H. gammarus* with ovaries at these stages did not exhibit such abdominal colouration.

Ovigerous setae found on pleopod endopodites and exopodites may be an indicator of sexual maturity in *Homarus spp.* The relationship between the appearance of these setae and female maturity and egg production is uncertain, although their development has been suggested to be

parallel to the gradual broadening of the abdomen (Aiken and Waddy, 1980). There are seven groups of setae found on pleopods as secondary sexual characteristics which increase the available surface area for egg retention. The use of ovigerous setae as an indicator of maturity was demonstrated to be valid in *Jasus spp.* (Annala *et al.*, 1980; Booth, 1984).

The development of "cement glands" on the pleopod endopodites (and additionally pleopod exopodites, protopodites and the sternal bars of the abdomen) of *Homarus spp.* has been shown to exhibit cyclic fluctuations with ovarian development and oviposition (Lloyd and Young, 1940; Aiken and Waddy, 1982). Cement gland development staging was used successfully by Ennis (1984) for *H. americanus*, but was not found to be an adequate method of determining a predisposition to becoming berried in *H. gammarus*, and would require further work on the understanding of cement gland development function before its use may be substantiated for field work on *H. gammarus* (Free, 1994).

The presence of a sperm plug, and potentially therefore a spermatophoric mass in the seminal receptacle of *H.* as an indicator of maturity is not thought to be reliable, and the method of examination may cause damage to females. Many sexually mature females do not carry spermatophores, and conversely, some individuals with spermatophoric masses in their seminal receptacles do not have adequately developed ovaries to indicate their maturity (Krouse, 1973; Aiken and Waddy, 1980). Cobb and Wang (1985) stated that female clawed lobsters can mate before ovarian maturity and then store sperm for up to two years; this will obviously complicate maturity estimates using this method and implies that, unlike males, females can mate while still both physiologically and functionally immature.

Variation in size at maturity

Regional variation in male size at onset of maturity has been identified in *H. americanus* using the Anderson cheliped index (AI) with both the immature male AIs and the mature AIs from different regions showing similar regression slopes (Aiken and Waddy (1980). Aiken and Waddy (1989) also showed regional variation in the onset of maturity using CPI for *H. americanus* from different areas in Canada. Templeman (1935) had also shown spatial variation in the sizes at male maturity of *H. americanus* using cheliped propodite length plotted against total length. Regional variation in male *H. gammarus* size at onset of maturity may also occur, although the difficulties in ascertaining size at onset of maturity using cheliped dimensions complicates quantitative assessment of such variation (Free, 1994).

The sizes at onset of maturity of both female *H. americanus* and *H. gammarus* have been shown to vary between locations. The size at first maturity of the American lobster varies between 55 mm CL in the western Long Island Sound (Briggs and Muschake, 1979) and 90 mm CL in the Bay of Fundy and southern Georges Bank (Templeman, 1939). Gibson (1969), using egg-bearing as the maturity indicator, observed different sizes at onset of maturity on the west and east coasts of the Irish Sea in *H. gammarus* (the smallest berried female from his pooled data-set was in the 70 to 74 mm CL size class). Free (1994) observed geographical variation in female size at onset of maturity using both the proportions of berried females (ranging from 78 to 119 mm CL) and the proportions of females with mature ovaries (stages 4+) (80 to 87mm CL). Both size at first maturity (smallest berried female) and size at 50 % maturity determined by ovary stage were found to be below MLS in some fisheries. Simpson (1961) showed differences in the size of 50% maturity between *H. gammarus* populations off

the north coast of Angelsey and Pwllheli, Wales. The size at maturity was smaller in the more shallow, warmer waters of Pwllheli (77 mm CL) than those of Angelsey (91 mm CL).

The causes of potential geographic and temporal differences in size at onset of maturity are difficult to determine and isolate. Higher temperatures are thought to contribute to early maturation of *H. americanus* (Aiken and Waddy, 1986), but this may also be caused by population density and fishing pressure (Aiken and Waddy, 1980; Cobb and Wang, 1985), or variability in growth rates which may influence the time taken to the onset of egg production (Annala *et al.*, 1980; Sastry, 1983, Wenner *et al.*, 1985). Accurate growth rate information (both moult frequency and increment) may help to determine whether size at onset of maturity is determined by age, instar or size at any given location. Cobb and Wang (1985) suggested that high population density and the selective pressure of high fishing effort (especially in cases where MLS is smaller than size at onset of maturity) may together exert a genetic pressure for maturation at a smaller size. A decrease in size at onset of maturity has been suggested for *Panulirus argus* in Bermuda from 90 mm CL to 81-82 mm CL, concurrent with an increase in exploitation rate between 1950 and 1986 (Sutcliffe, 1952; Evans, 1988). Variation in size at onset of maturity in other spiny lobster fisheries has been linked to water temperature (Annala *et al.*, 1980), variations in hydrological and physical environmental characteristics and their resultant density-dependent effects upon growth and mortality (Pollock, 1982) and population density (Chittleborough, 1974; 1976). In *H. americanus*, temperature is believed to be more important than animal density in determining size at onset of maturity (Aiken and Waddy, 1980).

The environmental factors that influence size at maturity need to be identified for the determination of the causes of both spatial and temporal variation in size at onset of maturity, for the resolution of an optimal minimum legal landing size. Regional comparisons of size at onset of maturity may need to consider the cause of potential spatial variation in maturity estimates. Individual age, size or instar may be determinants of sexual maturity. Size at onset of maturity is used for fisheries management considerations, but may not be as important as growth rate if either individual age or instar number determine sexual maturity. Lipcius (1985) suggested that a combination of age and size, within a narrow range of instars will determine the onset of maturity, rather than size alone. This would suggest that knowledge of moult frequency is crucial in estimating age at maturity, and of moult increment for estimating the resultant size at maturity.

Fecundity and egg development

Egg development

After oviposition, the eggs of *H. gammarus* are incubated for between 9 and 13 months (Branford, 1977; Free, 1994). Egg development during this period may be easily observed because of changes in colour (caused by caroteno-protein pigments) and the development of two large eyes. Perkins (1972) developed an eye index measurement to separate the eggs of *H. americanus* into development stages and to determine their development rate, which was shown to vary with temperature. Berried *H. americanus* females undertake seasonal migrations between shallow and deep water in order to improve their local temperature conditions during egg development (Campbell, 1986). Such migrations to warmer shallow waters may allow less developed eggs to catch up with well-developed eggs, thereby

decreasing intervals, between releases from different females (Attard and Hudon, 1987). No extensive migrations have been observed in female lobsters in the UK (Simpson, 1961; Jensen *et al.*, 1993).

Individual fecundity

Estimates of the fecundity of individual *H. americanus* suggest a logarithmic relationship between the number of eggs (clutch size) and carapace length (CL) (e.g. Herrick, 1909; Saila *et al.*, 1969; Perkins, 1971; Estrella and Cadrin, 1995; c.f. Squires, 1970). Clutch size has also been shown to vary between females of similar sizes in *H. americanus* (Squires, 1970).

H. gammarus appears to have a lower fecundity than *H. americanus* and the relationship between clutch size and carapace length in *H. gammarus* has been assessed as linear (Hepper and Gough, 1978; Latrouite *et al.*, 1984; Bennett and Howard, 1987; Roberts, 1993; Free, 1994). The size range of females used in the of *H. gammarus* have necessarily been restricted because of the restricted size range of lobsters in European fisheries, and this may influence the lack of any curvilinear relationship between clutch size and CL. Squires' (1970) study of *H. americanus* also examined a truncated size distribution of females and estimated a linear relationship between the two variables. Free (1994) suggested that either a linear or 2nd order polynomial regression would adequately describe the relationship between clutch size and female CL but that a wider size range of female *H. gammarus* would need to be examined to confirm the preferred model. A linear model was therefore preferred for statistical simplicity.

Variation in fecundity

Differences between estimates of fecundity in *H. americanus* (i.e. individual clutch size) have been attributed to methodology and geographical location by Aiken and Waddy (1980), but may also be caused by estimates being made at different stages of egg development. Both spatial and temporal variation in individual lobster fecundity has been observed between *H. americanus* populations (Aiken and Waddy, 1980; Estrella and Cadrin, 1995). Aiken and Waddy (1986) hypothesised that the apparent influence of location upon fecundity is most probably an indirect effect owing to variation in local environmental conditions. Ennis (1981) commented that potential spatial variation in lobster clutch sizes may be difficult to analyse because of geographical differences in size at onset of maturity and the importance of size-fecundity relationships. Annala and Bycroft (1987) did not find any geographical variations in the fecundity of the palinurid *Jasus edwardsii,* but did suggest a potential, local variation in clutch size because of food availability.

The small number of studies on *H. gammarus* fecundity had previously prevented conclusions from being drawn about possible geographic and spatial variation in clutch sizes, as has been shown to occur in *H. americanus.* Free (1994) analysed size fecundity data from sites around England and Wales and found both between-site and between-year variation for *H. gammarus* females. Estimates of fecundity in Yorkshire and Sussex by Free (1994) were higher than those suggested by both Hepper and Gough (1978) and Bennett and Howard (1987) (Free *et al.*, 1992) (Table 4). Apparent differences in fecundity between sample sites and dates may be accentuated by individual variation in clutch size or differences in the size ranges of the females studied on each sampling trip. Spatial and temporal variations in fecundity may be

caused by local environmental conditions (such as seawater temperature or food availability) or density-dependent factors, which may also be affected by the intensity of fishing effort.

Table 4 Fecundity estimates of *H. gammarus*
Tabell 4 Fekunditet mål for H. gammarus

Author	Location	Egg development stage	Fecundity estimate
Hepper and Gough (1978)	North Wales	Eyed	217.74CL-2490.3
Latrouite *et.al* (1984)	Brittany	Eyed	305CL-22759
Bennett and Howard (1987)	Yorkshire	Non-eyed	247.5CL-9629
Bennett and Howard (1987)	South Wales	Non-eyed	430.8CL-32782
Bennett and Howard (1987)	South Wales	Eyed	430.8CL-35872
Roberts (1993)	Dorset	Eyed	400.2CL-2746.1
Free (1994)	Sussex 1989	Non eyed	226.3CL- 10972.3
Free (1994)	Sussex 1991	Eyed	225.7CL-11951.9
Free (1994)	Yorkshire 1987	Non-eyed	394.6CL-28606
Free (1994)	Yorkshire 1990	Non-eyed	272.6CL- 15675.3
Free (1994)	Yorkshire 1988	Eyed	363.2CL-23899.5
Free (1994)	Yorkshire 1991	Eyed	369.4CL-23831.3

Egg loss
Estimates of the individual fecundity of *Homarus ssp.* are influenced by egg loss during the incubation period which may be caused by attrition, unfavourable social conditions or parasitism (Perkins, 1971; Aiken and Waddy, 1980; Campbell and Robinson, 1983). Although *H. americanus* egg masses have been shown to be subject to infestations of the nemertean parasite *Pseudocarcinonemertes homari* (Campbell and Brattey, 1986), which may result in partial or even complete egg loss, there is no indication that this parasite occurs around the British coast at present. Egg loss attributed to other factors has been shown to average 36% in *H. americanus* (Perkins, 1971), 27% in *H. gammarus* (Latrouite *et al.*, 1984) and 45%, from oocyte numbers within the ovary (potential fecundity) to full development, in *Nephrops norvegicus* (Morizur *et al.*, 1981). Estimates of individual fecundity in both the American and European lobsters must therefore take the development stage of the eggs into account, and most studies have therefore used the number of eggs carried by females toward the end of incubation in fecundity estimates (Perkins, 1971; Hepper and Gough, 1978). Bennett and Howard (1987) observed a decrease in egg loss with increasing female size for *H. gammarus* in South Wales (58 % at 90 mm CL and 11 % at 150 mm CL). Free (1994) found that egg loss varied considerably between individuals, but with no apparent relationship between the number of eggs lost and female size.

Female size and energetic investment
In addition to increases in egg number, an increase in egg size may also be observed with increasing female size in *H. gammarus* (Latrouite *et al.*, 1984). This is a further indication of the greater degree of female energetic investment in her brood as size increase. Eggs from larger *H. americanus* females have also been shown to be larger, and to have a higher energy content (Attard and Hudon, 1987). They suggested that smaller females would allocate more

resources to somatic growth, whereas larger females would divert their energy investment away from reproductive processes and towards maintenance-orientated functions. Attard and Hudon (1987) concluded that the larger females, with a greater number of eggs containing relatively more calories than those of smaller females, would effectively contribute even more to lobster recruitment than their greater fecundity would suggest. This is because of the increased chances of survival of by larger eggs with an earlier extrusion date and hatching time. The time of egg extrusion, number of eggs, female size and energy content of those eggs at different stages during the female's life span, might all affect larval survival rates. Survival rates of larvae from larger females may be increased because of the higher energetic investment put into the eggs (Attard and Hudon, 1987; Sasaki *et al.*, 1986).

Spawning frequency and individual fecundity

Measurements of the individual fecundity of decapod crustaceans usually refer to clutch size (Barnes and Barnes, 1968). For fisheries studies, however, population fecundity is more relevant to understanding potential stock and recruitment relationships. The number of eggs per recruit is influenced by the timing of the fishing season, recruit size, fishing mortality, size at onset of maturity and growth rate (Campbell and Robinson, 1983). Egg production was found to be regulated by density-dependent factors in the palinurid lobster *Palinurus longipes cygnus*, with a high population density resulting in smaller sizes at maturity with fewer eggs per clutch and fewer clutches per year (Chittleborough, 1976). Estimating spawning frequency in *Homarus spp.* is more complicated than for most palinurids, as the basic ovarian cycle is two years long (Aiken and Waddy, 1976), and only a proportion of females can therefore be expected to carry eggs in any given year; in addition the catchability of berried females is thought to be lower than that of non-berried individuals, (Templeman and Tibbo, 1945; Hallbäck and Warren, 1972; Squires *et al.*, 1974; Branford, 1977).

Fecundity is a product of breeding frequency and the number of young produced per breeding cycle (Chittleborough, 1976). Each of these factors may respond independently to changes in environmental conditions. Spawning frequency is affected when animal density is high and female nutritional state is poor, whereas the number of young produced is related to female size and is therefore affected by growth rates (Chittleborough, 1976).

Summary

The use of cheliped dimensions as external indicators of maturity in male *H. gammarus* has not been as successful in the determination of the size at maturity, as it has in *H. americanus.* Free (1994) suggested that further work is required in order to relate both size at physiological and functional maturity to suggested inflection points, and intersections produced when such external indicators of maturity (i.e. AI, CPL, CPI) are plotted against CL. Internal indices of female maturity (i.e. OVF, ROW and ovary weight) are all destructive methods of maturity determination, and individual inconsistencies in these factors suggest that accurate ovary stage determination, using gross morphology indices, may be the simplest and most useful method of assessing female physiological maturity. The increase in variability of these internal indices with increasing CL and AW indicated by Free (1994) also suggests the preferential use of ovary development stage for the determination of physiological and functional maturity in *H. gammarus.* Geographical variation in size at onset of maturity has been observed in *H. gammarus*, although future studies using specimens collected from a wider range of locations may assist in the determination of the factors that cause spatial variability in size at onset of maturity.

The true relationship between clutch size and female CL in *H. gammarus* is still unclear because of the restricted size ranges of the females examined. Until this relationship has been fully determined, it will not be possible to evaluate the relative contribution of the largest females to population fecundity. However, the linear model currently used to describe the relationship between clutch size and female CL adequate until proven otherwise.

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Lobster maturation and fecundity

Discussions

The discussion started from whether the common assumption in lobster reproductive dynamics that females of a given size have equal potential to contribute to stocks is true. Evidence indicates that female size at onset of maturity and size/fecundity relationships can vary with site and between years. The reasons for this are unknown, but water temperature and animal density may be implicated.

There is a lack of information on changes in the frequency of spawning with size or age of females so the lifetime egg contribution of a female cannot be reliably estimated. Presence of setae is a good indicator of maturity but their presence does not mean that eggs will be extruded that year. Once mature, *Homarus gammarus* females spawn every other year until some point when the frequency changes to twice every three years. Models of reproductive dynamics would benefit from knowledge of when this change occurs.

These variations point to the need to carefully consider sampling and estimating protocols and the need for standardised approaches between areas so that results are comparable.

It is often assumed that all eggs have equal potential to contribute to the next generation. Again, this assumption may not apply.

There is growing evidence from laboratory studies to suggest that there are real differences in egg quality (measurable as biochemical composition, energy/lipid content, or subsequent larval viability) both within and between broods. These differences might arise as a result of

a) differences in egg size, which in turn may be correlated with female size,

b) differences in maternal nutrition during egg formation,

c) adverse environmental conditions experienced during incubation (e.g., egg development is extended and egg loss increased at low salinity), and

d) the position and rate of development of eggs within a clutch.

Whether these variations seen in the laboratory persist in the field needs to be tested. Models of reproductive dynamics aid in management of lobster fisheries and could take into account such variation in the quality (condition) of eggs. Sensitivity analyses can indicate which variables have most impact on estimates derived from these models.

Protecting large females may lead to higher overall egg production because of their disproportional high egg contribution. Manipulating legal sizes in a fishery (e.g., protecting large females, changing minimum legal sizes) may, however, have adverse effects on fertilisation success. If large females depends on large males for successful fertilisation of the eggs, a female-biased population, due to protection of productive females, might be less productive. It is important that the fishery is monitored to ensure that reproductive rates do not fall as a result of any such changes.

Age determination and modult histories in lobsters

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The discontinuous mode of growth in crustaceans means that data are required on both moult frequency and moult increment if growth curves are to be obtained. The determination of both of these parameters is complicated by a number of factors. Both vary with the age or size of the individual. In general, moult frequency is higher in the younger stages and moult frequency declines with age. In species such as *Nephrops norvegicus* there can be marked differences between the sexes with respect to both parameters. In addition, environmental factors such as the availability of food, appendage loss and ambient temperature may affect the size of the moult increment and the frequency of moults. Hartnoll (1982) has reviewed four methods for the construction of growth curves for crustaceans and the problems related to each. The methods include: a) Monitoring the growth of captive individuals; b) Monitoring the growth of wild individuals by tagging and recapture methods; c) Size-frequency analysis of growth curves from increment and intermoult data. d) Synthesis of growth curves from increment and intermoult duration data. To these we can add: e) Age pigment-frequency analysis to identify modes (Sheehy *et al.*, 1994). Each method has certain shortcomings. a) Data derived from monitoring the growth of captive individuals cannot be used for species such as lobsters where the life cycle is long and the culture conditions are likely to be significantly different from those in the wild. b) Tagging and recapture methods require massive effort and it is difficult to monitor all life stages because of the size-selective methods of capture. Tags may be lost and could affect growth rates or the ability to moult successfully. c) Size frequency analysis has proved useful for certain species. However, for decapods, the method is only likely to be able to reliably discriminate the first 9 or 10 instars (Hartnoll, 1982). For *Homarus gammarus*, the long life cycle and variability in growth rates between individuals makes the technique difficult to apply to large lobsters. d) Synthesis of growth curves from increment and intermoult duration data depends on obtaining reliable data for both parameters. Both types of are difficult to obtain. For wild lobsters in a fishery the most likely source of data concerning moult increment would be from tag returns. Reliable intermoult duration data are particularly difficult to obtain. Once again tagged individuals can be used to measure the increment between release and recapture. For a variety of species it has been obtained in the past from captive individuals. However, data gathered in this way must be treated with caution. Another approach is to record the frequency of moulting individuals in a large sample held in captivity for one or two days after capture.

A variety of approaches have been used to obtain data for determining moult stadium, moult duration increment and absolute age.

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Anatomical markers of moult stadium

Certain structures increase in size or complexity with age. If such a feature could be identified where there are moult-stage-specific changes in anatomy, this could be useful for growth curve construction because it would help with age estimates of wild-caught specimens (provided that the relevant moult-frequency data were available).

In crabs, the number of lamellae in the crab endocuticle in individuals preserved at Drach stage C_4 increases with size. Yano & Kobayashi (1969) were able to discriminate four age classes in a group of 100 wild-caught crabs (*Gaetice depressus*) with carapace lengths ranging from 6.5 - 24.5 mm. Attempts to use a similar method on *N. norvegius* were unsuccessful (Farmer, 1973) and this method is unlikely to be useful for *H. gammarus*.
Two studies using anatomical features to determine moult stage have been aimed specifically at the European lobster.

The arthropodan compound eye grows by recruitment of new ommatidia to the margin of the eye at each moult (Parker, 1890). This is very clear in juvenile stages and probably continues throughout life. In a laboratory study of juvenile lobsters at moult stages 6-12 it was shown that the eye grows isometrically with respect to carapace length and that there is a steady increase in the number of ommatidia with eye growth (Shelton *et al.*, 1981). However, counting ommatidia in these young lobsters only allowed discrimination to the nearest two moult stages. It was concluded that the number of ommatidia depends on the lobster's size rather than its moult stage. Because of the variability in growth rates between individuals, the method is likely to be very unreliable for moult stage determination in older lobsters.

Another method that may be useful in determining moult stages in juvenile lobsters involves counting the numbers of segments in the exopodite of the antennule. Henocque (1987) showed that up to moult stage 15 there was a very strong correlation between the number of segments and moult stage so that counting segments allowed discrimination between juvenile stages. For more mature lobsters (carapace lengths 40-140 mm) it was only possible to examine the relationship between number of segments and carapace lengths because data on moult stages were unavailable. Here, there was a much poorer correlation between the numbers of segments and carapace lengths than in the juvenile stages. In addition, in wild-caught lobsters, damage, and subsequent regeneration of damaged antennules would alter the number of segments. At present, the method based on counting antennule exopodite segments has not been researched sufficient in detail to make it worth using.

Age determination using $^{228}Th/^{228}Ra$ chronology

Although there is no reliable anatomical marker for total age, a method that depends on the $^{228}Th/^{228}Ra$ ratio in the exoskeleton has been used to measure the time that has passed since the previous moult (Le Foll *et al.*, 1989). The technique could be used to determine moult frequency. The method depends upon the fact that radium from the seawater is taken into the exoskeleton as it is laid down and that radium from exoskeletons of the previous instar is not. Once incorporated the radium decays to thorium. The method requires meticulous preparation methods and apparatus that is neither cheap nor easily available; the accuracy is between 15-20% using specimens of known age. If it were used for determining the time between moults of wild-caught specimens that were in intermoult, additional errors would come from estimating the time remaining until the next moult.

A moult recording tag

One method for obtaining information on moult increments and frequencies involves the use of a living tag (Shelton & Chapman, 1987; 1995). This can be used in conjunction with conventional tag and release methods. The method is known to work in both *N. norvegicus* and *H. gammarus,* and involves the implantation of a 2 x 4mm piece of donor integument (cuticle + epidermis) into the haemocoel of a recipient whose moult history is to be followed. Once inside the recipient, the implant forms a cyst with cuticle in the middle surrounded by the epidermis (fig 1.) The epidermis in such cysts continues to lay down cuticle in step with the host. When the host moults, the cyst sheds the cuticle layer towards the inside of the cyst. On recapture, the number of moults since release can be determined by counting the cuticle layers within the cyst. This method can provide data on moult frequency and moult increment. Like all tag and release methods, however, it requires a major effort to obtain data for all size ranges.

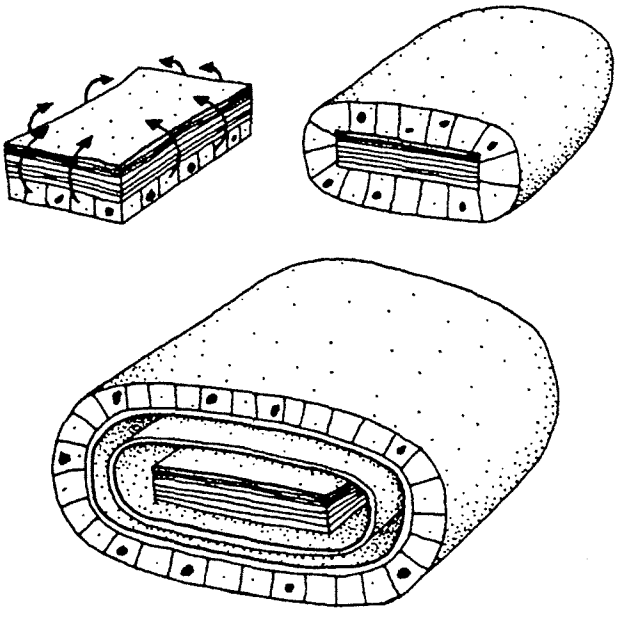

Figure 1 Semi-schematic diagram to show the development of a multilayered cist. (P.M.J. Shelton, University of Leicesteer, UK)

Figur 1 Skjematisk skisse som viser utviklingen av syste med flere skall-lag (P.M.J. Shelton, University of Leicesteer, UK)

Age pigment studies in lobsters

Lipofuscin occurs in the autofluorescent, lipid-rich, heterogeneous granules that accumulate in the cytoplasm of cells in post-mitotic tissues (fig 2.). Although its structure and biochemical composition are poorly understood, considerable evidence supports the view that lipofuscin is formed as a result of *in vivo* lipid peroxidation of organelles. It is regarded as being a universal indictor of animal senescence (Tsuchida *et al.*, 1987). Although a relationship between ageing and lipofuscin accumulation has been known for over a century, it was not until the work of Ettershank (1983) that the measurement of the abundance of lipofuscin in the post-mitotic tissues of crustaceans was employed to estimate the age structure of crustacean populations. Despite promising results, a definite age-dependent (as opposed to growth-dependent) accumulation of solvent-extracted lipofuscin was not shown and doubt has since been cast

over the reliability of the whole spectrofluorimetric assay method as no study has yet demonstrated that extracted fluorescence is in fact derived from morphological lipofuscin. Sheehy (1989) demonstrated lipofuscin granules in histological sections of a crustacean brain for the first time and has since presented convincing evidence that the measurement of morphological lipofuscin has the potential to be a superior predictor of age than conventional morphometric analysis (Sheehy, 1990).

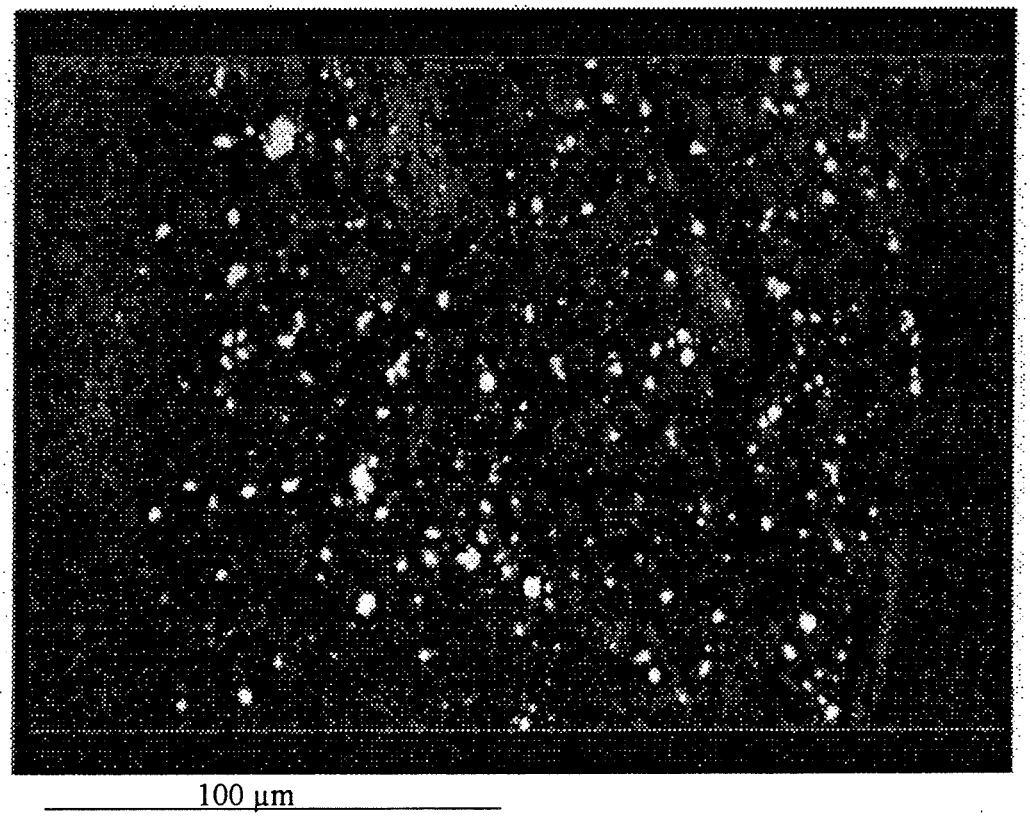

Figure 2 6µm section of the brain of *H. gammarus* showing brightly fluorescing granules. (M. Belchier, University of Leicester, UK).

Figur 2 *6µm seksjon av en hummerhjerne der lipofuscin granulatene vises som lyse flekker (M. Belchier, University of Leicester, UK).*

Morphological lipofuscin has been demonstrated in the brains of several species of large decapod crustaceans of commercial importance, including the European lobster, *H. gammarus* (Sheehy and Wickins, 1994) and the Norwegian lobster, *N. norvegicus* (Belchier, *et al.*, 1994). A larg- scale study of the accumulation of lipofuscin in the brains of *H. gammarus* using specimen of known age from an extensive MAFF tag-recapture programme has been made and the results demonstrate a superior correlation between age and lipofuscin concentration than between age and carapace length at all the sites examined. Using this information it should now be possible to sample a large wild population of *H. gammarus* and assay for lipofuscin concentration using morphological methods and image analysis to enable differentiation of age classes and hence give a clearer idea of the age structure of the population. The ability to discriminate between cohorts will also facilitate the construction of accurate growth curves for the species under examination. Sheehy *et al.* (1994) have shown

improved discrimination of age classes in a wild population of *Cherax quadricarinatus* and in the Western rock lobster *Panulirus cygnus* (Sheehy, pers. comm.).

Both chemical extraction, and histological preparation of lipofuscin involve chemical treatment of the material. Since the lipofuscins are autofluorescent, optical sectioning of fresh material offers a potentially more accurate method of assessing the lipofuscin concentration without chemical intervention. In addition, brains can be examined and the lipofuscin levels quantified much more rapidly than by either solvent extraction or histological methods. This is an important consideration when large sample sizes (>200 individuals) are required for accurate predictive modelling of the age structure of crustacean populations. Belchier *et al.* (1994) have shown a good correlation between lipofuscin concentrations assessed by confocal microscopy and conventional histological preparation in the brain of the Norway lobster *N. norvegicus*. It is hoped that a non-destructive method of lipofuscin assay will be developed for crustacea in order to enable commercial catches to be sampled in much the same way as length/weight measurements are currently recorded for a fishery.

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Growth and ageing in lobsters

Discussions

The discussion emphasised how important age estimation and growth studies are in lobster fishery management, in understanding reproductive biology, and in seeding programmes. Knowledge of age structure is crucial to stock-recruitment studies and in the identification of cohorts. The techniques of cuticle implantation and measure of accumulated fluorescent brain pigments were seen by the meeting as being of great potential use in understanding processes and interactions where age of the animal is important.

The discussion centred on the use of the two ageing techniques. Cuticle implanting is the best developed of the two and has been field tested.Techniques need to be standardised so that results are comparable between areas. Statistical methods should be explored to deal with size and lipofuscin quantity as independent correlates of age.

Use of the fluorescent pigment technique is being tested in Norway, in 1995-1996, on lobsters released as juveniles at Kvitsøy, with tags to confirm their age at recapture. The results seems promising according to age estimation, but it is based on a slow and difficult analysis.

At the meeting it was felt that both techniques should be tried simultaneously. The meeting resulted in a later co-operation between Dr. Shelton, Leicester University and Mr. I. Uglem, Institute of Marine Research, using cuticle implantation in lobsters in the well monitored Kvitsøy population.

A trans-atlantic perspective on *Homarus* recruitment & enhancement

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Introduction

Early life history and recruitment processes have been surprisingly enigmatic for researchers studying *Homarus*. It is only relatively recently that the distribution and abundance of newly settled *Homarus americanus* has been quantified in the wild; equivalent data for *Homarus gammarus* remain more elusive. Recent progress in understanding the ecology of the early life phases of the American lobster may provide a useful model for the European lobster. With North American harvests of *Homarus* about 30 - 40 times greater than total European landings (Fig. 1), there appears to be great potential for stock enhancement in Europe. But we should be careful how far we take the European - American comparison because there exist differences between eastern and western Atlantic fauna of rocky habitats that could impact lobster recruitment. Here I briefly summarize recent developments in our understanding of processes operating during the early benthic life of the American lobster that are critical to recruitment and relevant to the efficacy of stock enhancement. Next, I make a trans-Atlantic comparison of the fauna of cobble habitats from recent suction samples. The comparison reveals dramatically higher species diversity but lower numbers of *Homarus* in Europe than in New England, a situation that may warrant a closer look at the potential impact of species interactions on lobster recruitment and stock enhancement.

Ecological phases of lobster life history

The life histories of *H. americanus* and *H. gammarus* are fundamentally the same. Ecological transitions during the life history are decoupled from specific molt events, so it is helpful to make the distinction between molt stages and ecological phases (Cobb and Wahle, 1994). In clawed lobsters the first ecological phase, the pelagic phase, includes three larval and one postlarval stages and terminates at settlement. Once the animal establish on the bottom the transition to the early benthic phase has been made. This phase is cryptic, relatively sedentary, and the most habitat-restricted segment of the life history. Lobsters generally become more emergent, however, as they grow. Two subsequent phases are defined in terms of reproductive status (Steneck, 1989): the adolescent phase, since *Homarus* is not yet sexually mature as it becomes more emergent; and the reproductive phase, since the onset of maturity occurs over several molts and is accompanied by sexual differences in behavior, agility, and allometric growth (Aiken and Waddy, 1980).

Early life history and recruitment processes

Here I focus on processes occurring early in the life history because cohort success is often determined at that time, and as a practical matter for fisheries managers, it is desirable to predict fluctuations in recruitment to the fishery as far in advance as possible. Recent advances in our ability to census newly settled lobsters by airlift suction sampling has opened a previously unavailable window on spatial and temporal patterns of benthic recruitment not previously available (Able *et al.*, 1988; Wahle and Steneck, 1991; Incze and Wahle, 1991).

Early benthic phase American lobsters are the most habitat-restricted segment of the life history in their association with cobble-boulder habitats. They prefer to occupy the interstices of rocks or other existing shelters although they are capable of constructing burrows in cohesive mud with no existing structure (Berrill and Stewart, 1973; Wahle, 1992a; Wahle and Steneck, 1992). This habitat selectivity is likely to be reinforced by the high rates of predation on small lobsters with no shelter. Laboratory and field studies have implicated a host of fish and crab predators (Lavalli and Barshaw, 1986, Wahle and Steneck, 1992). One field study of video-monitored tethered lobsters reported the median latency of attack by fish at 15 minutes (Wahle and Steneck, 1992), far less time than it takes to construct a new burrow.

Because of the success in censusing newly settled lobsters, my co-workers and I have been monitoring temporal and spatial patterns in settlement in two regions of New England, Rhode Island and the central Maine coast since 1989. The long-term goal of the monitoring is to determine whether a settlement index may be a useful forecasting tool for trends in the fishery, as it is for the western rock lobster fishery in Australia (Phillips *et al.*, 1986).

The emerging patterns of settlement have been the basis for hypotheses on the mechanisms that affect recruitment and the fate of benthic cohorts on local and regional scales. Several studies point to the importance of large-scale circulation patterns, wind, and postlarval swimming to transport and settlement patterns of the American lobster (Ennis, 1986, Hudon *et al.*, 1986; Katz *et al.*, 1994; Wahle and Incze, in review). Local differences in population density determined by larval supply persist for only a year or so, after which they tend to smooth suggesting a net movement from areas of high concentration to low (Wahle and Incze, in review). Further field experiments indicate that these movements away from high-density sites may be due to crowding effects that set in as lobsters grow (Wahle and Incze, in review). It must not be forgotten, however, that shelter size constraints (Barry and Wickins, 1992, Wahle, 1992a), growing nutritional demands (Lawton, 1987), and the declining risk of predation (Wahle, 1992b) could have the same effect on movements from the initial recruitment site. It will be important for future research to elucidate the mechanisms that affect the size-specific propensity to disperse.

Do associated fauna affect recruitment? A trans-Atlantic perspective

While we are beginning to understand how larval supply and habitat quality influence patterns of benthic recruitment, remarkably little is known about the interactions of lobsters with coexisting fauna. Suction sampling has also provided data on the diversity and abundance of associated fauna. The trans-Atlantic comparison provides a larger biogeographic perspective revealing dramatically higher species diversity, but lower numbers of *Homarus* in Europe than in New England, a situation that might warrant a closer look at potential species interactions.

In the autumn of 1994, John Mercer at University College Galway, Ireland coordinated a series of dive surveys of sites in the southwestern part of that country, where a lobster stock enhancement program was ending its second year of hatchery releases. I also traveled to the Channel Islands, UK, which, for their small size, boast some of the largest lobster landings in Europe. The lack of reports of newly settled European lobsters in the wild provided an added challenge for our efforts. We sampled eight sites in three study areas, and here I briefly compare the diversity, abundance, and sizes of taxa to what we see with a equivalent sampling effort in cobble beds in New England. Here I restrict the report to shelter-dwelling decapods, other than hermit crabs, that inhabit cobbles during part or all of their lives.

In New England taxonomic diversity is relatively low (Fig. 1). In the Gulf of Maine, *H. americanus* and *Cancer irroratus*, the rock crab, are by far the two most abundant subtidal species in cobble. (*Carcinus maenas,* the green crab, is more abundant intertidally). *Cancer borealis*, the Jonah crab, common in traps as adults, is found extremely rarely as a juvenile and remains an enigma. In the northern Gulf of Maine these decapods were far less abundant than to the south and west, a historic pattern that some suspect may be related to circulation and cold temperatures in that region. In southern New England however, xanthid crabs add to the mix of decapods, and tend to be most abundant where *Cancer* is not.

In Ireland and the Channel Islands, in contrast, species diversity was much higher (Fig. 1). But while *Homarus* and *Cancer* were most abundant genera on the American side, they were least abundant in Europe despite major fisheries for both groups. Four other decapod families dominated: xanthid crabs, galatheids, porcellanids and alpheids with at least two to three species identified in each family. We found no newly settled *H. gammarus*, however, even at the Irish release sites. Despite these differences in faunal composition, the collective densities of these groups were similar on both sides of the Atlantic, ranging between 20-80 individuals per square meter.

Small individuals dominated the populations of these cobble-dwelling taxa (Fig. 2). All had size modes between 5 and 15 mm in carapace length or width which for at least the porcelain crabs, xanthid crabs, and snapping shrimp approximates the adult size. Only those species that grow much larger (i.e., > 30-40 mm), like lobsters and *Cancer spp.*, do not maintain a life-long association with cobble.

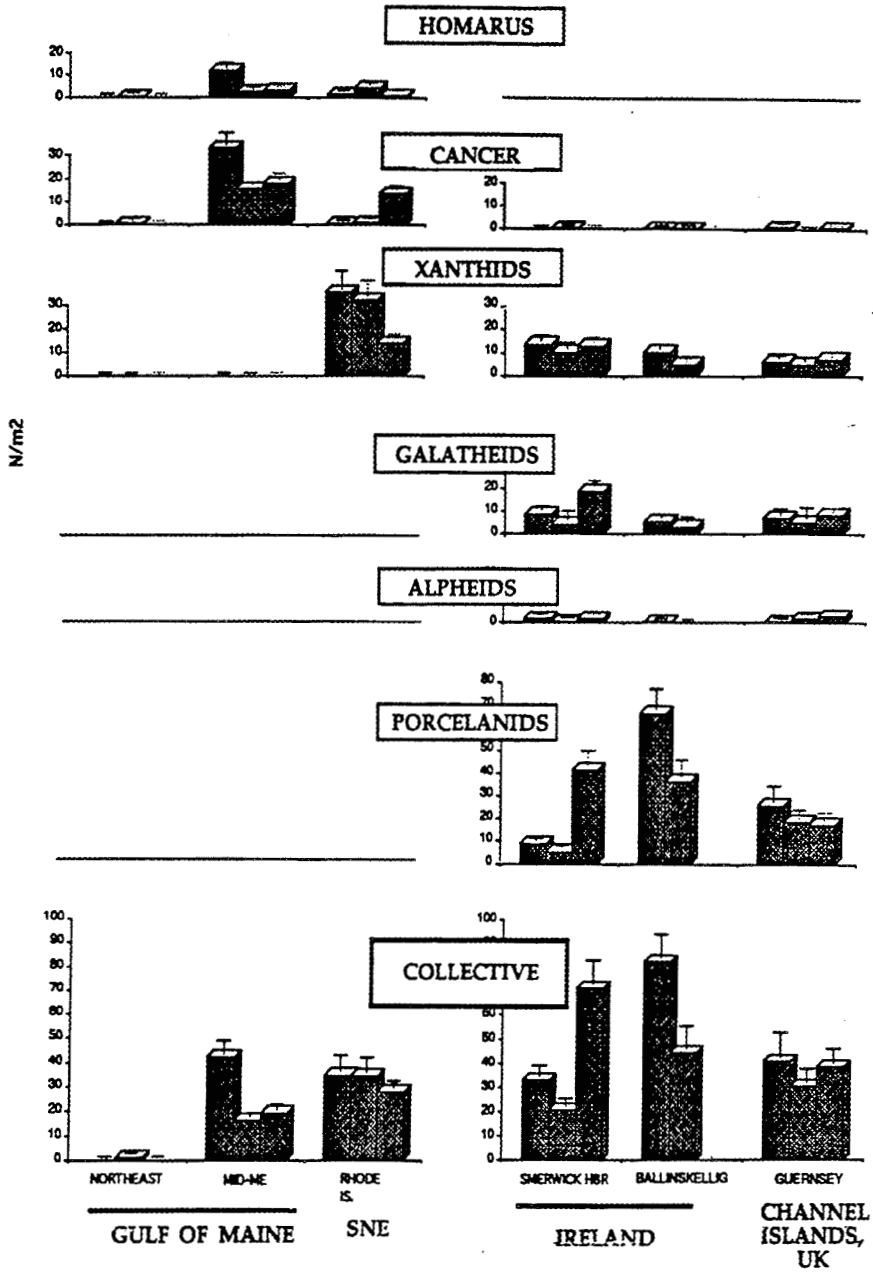

Figure 1 Average population densities (+ 1SE) of decapod fauna in cobble habitats of New England and Ireland/Channel Islands. Each bar represents a study site where twelve 0.5 m^2 quadrates were suction sampled. SNE = southern New England.

Figur 1 Gjennomsnittlig populasjonstetthet (+1SE) av dekapodfauna i kultsteinhabitat utenfor New England og Irland/Kanaløyene. Hver søyle representerer et felt område der tolv 0.5 m^2 kvadratruter har blitt «støvsugd». SNE= Sørlige New England

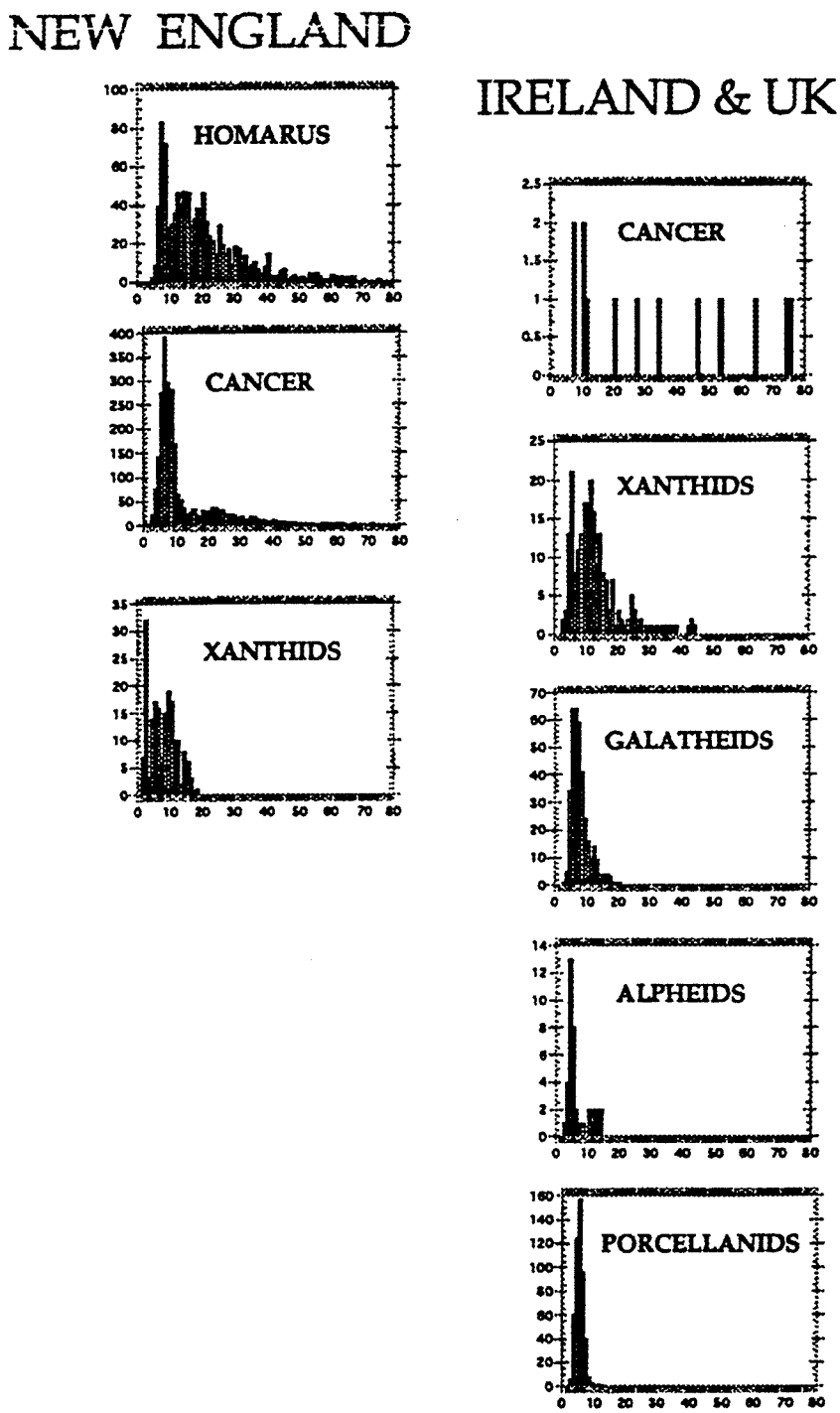

Figure 2 Representative size composition of decapod populations from cobble habitats in New England and Ireland/Channel Islands.

Figur 2 *Representativ størrelses sammensetning av dekapodpopulasjoner i kultstein-habitater utenfor New England og Irland/Kanaløyene.*

Where were the young lobsters? If commercial landings are a reasonable index of abundance, it is very possible that our sampling effort was inadequate to detect measurable densities of *H. gammarus*. Recent landings of *H. gammarus* throughout Europe have been only about 1/40th of North American landings (Fig. 3; FAO Yearbook, 1992), about equivalent to the landings of the state of Rhode Island. (Ireland and the UK account for about 75% of Europe's landings). Densities of lobsters of all sizes in American cobble beds average about 1-3/m^2; and one-fortieth of that would give a density of 0.02 - 0.07 /m^2. At that density, according to Poisson analysis, on average we would expect our sampling effort of 108 half-square-meter quadrates to produce 106 quadrates with no lobsters, two with one lobster, and none with two or more. By this admittedly coarse analysis with no correction for fishing effort or coast length, we might have expected very few lobsters to begin with. Our less systematic visual searches, totaling five additional dive-hours, did produce two lobsters: a large berried female at 110 mm CL, and a juvenile at 40 mm.

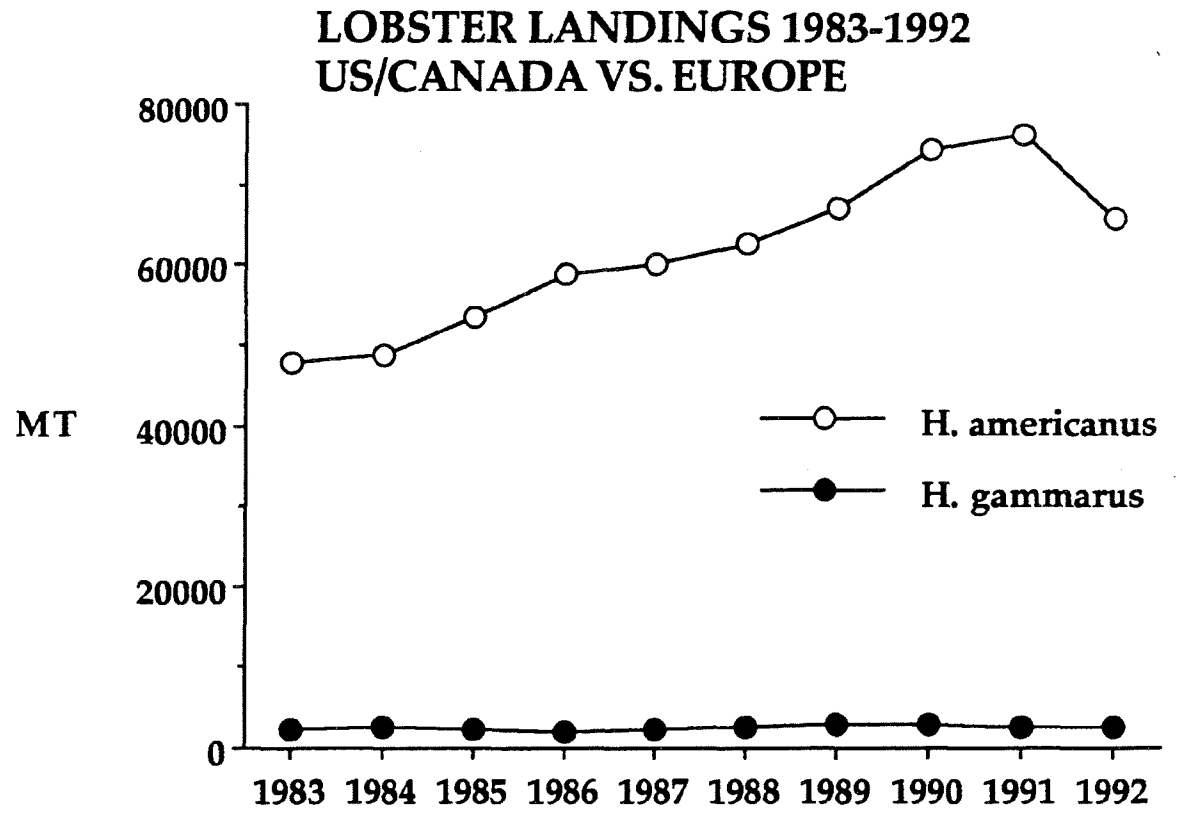

Figure 3 Lobster landings in North America (*H. americanus*) and Europe (*H. gammarus*). Source: United Nations Food & Agriculture Organization Yearbook, 1992.

Figur 3 *Registerte hummerleveranser i Nord Amerika (H. americanus) og Europa (H. gammarus). United Nations Food & Agriculture Organization Yearbook, 1992.*

Why would the European lobster be so rare in cobble if it is so ecologically similar to the American lobster, as we have assumed? There are several hypotheses. First, fishing has undoubtedly depleted stocks, and although there is a minimum harvestable size, there is no consistent protection for egg-bearing females throughout the species range, so larval

production is likely to be quite low. But that explanation seems insufficient to explain the absence of new recruits at the Irish release sites that had been seeded with tens of thousands of hatchery-reared lobsters over two years.

A second hypothesis is that postlarval *H. gammarus* is not as ecologically similar to *H. americanus* as we have assumed, and that it may prefer a nursery habitat other than cobble. That explanation also seems unlikely, however, given the similarity to *H. americanus* in shelter-seeking behavior and habitat preference (Berrill, 1974; Howard and Bennett, 1979; Howard, 1980). All the early benthic phase *H. gammarus* in a seawater pond at the hatchery were under rocks, shells, and plastic trays placed on the bottom for cover. Moreover, with the greater sampling effort that has gone into other habitats over the years, such as sediment coring, for example, one is hard pressed to think what other habitat they might occupy.

A third hypothesis is that interactions with other species might inhibit successful recruitment to the benthos. This explanation seems consistent with the previous evidence. There are, however, many unknowns regarding species interactions in these habitats. Is the interaction predatory or competitive? If it is competitive, shelter may be a limiting resource, but we know very little about the carrying capacity of these habitats for *H. gammarus*. For the American lobster, however, we have determined carrying capacity through saturation seeding experiments of standardized cobble plots in which we can manipulate the quantity of cobble to assess its effect on numbers (Wahle & Incze, in review). From those experiments carrying capacity is estimated to be as high as the highest benthic recruitment density we have seen in nature, around 5 - 6/ m^2 for newly settled lobsters, still lower than you might expect given the large number of crevices available in cobble beds. This low putative carrying capacity suggests that there are space requirements beyond shelter which we do not yet understand for the American lobster, much less for the other species.

Conclusions

There is no doubt that strong parallels exist in the life histories and ecologies of the American and European lobster. Indeed the two species are capable of hybridizing in captivity. The rocky habitats they occupy are even quite similar. There are, however, striking faunistic differences that need to be examined for their potential impact on lobster recruitment. The decapod taxa have similar habitat requirements, but there is little knowledge of the nature of the interaction. It will be important to devise models and experiments to test these hypotheses because the benefit will be a greater insight into the recruitment process as well as the efficacy of stock enhancement. In any case, there seems to be a need to go beyond the single-species approach if we are to fully understand the factors that influence recruitment of *Homarus*.

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Recruitment of early benthic stage lobster juveniles

Discussions

Most of what is known about the biology of the early life history stages of the lobster, and the effects of external variables on these stages, is learned from laboratory studies and from laboratory rearing. Little is known about these stages in nature. For example, it is unknown where and when most settlement of larvae takes place. It is assumed that juveniles seek shelter after settlement, presumably to avoid predators and to make use of local food resources. More information is critical to fishery management and to seeding programmes.

The major issue in this discussion concerned the cost-effectiveness of direct field observation compared with field manipulation experiments when determining larval recruitment and juvenile processes. Manipulation experiments might involve the seeding of young juveniles in field plots and the tracking of their survival over time. 'Bottlenecks', where survival is limited by habitat availability, food, or some other factor, need to be identified. Such studies as these can also show the optimal sites for commercial stocking.

Releases into study sites should be made at the most appropriate time of the day and in the right season so as to enhance survival. However, the fact that seeded animals usually cannot be found after release could mean that lobsters from manipulation experiments may not be recovered for some time. There is therefore a case for manipulation experiments being supplemented by direct field observation of larvae and juveniles. Field studies should include the use of collectors such as those found effective for clawed lobsters in North America because collectors can give valuable information on depth, areas, times, and densities of settlement.

Studies are needed into the potential interactions between *Homarus gammarus* and the array of potential competitors present at high densities and having similar habitat requirements.

Norway being at the northern limit of distribution of *H. gammarus* may be a special case with regard to larval recruitment processes. In particular, the effects of variation in water temperature on larval development rates and settlement may be more marked in Norway than elsewhere, these variations possibly bringing about large changes in settlement from year to year. This issue requires study.

Some interesting accounts of juvenile occurrence need follow-up: in both Norway and Sweden, significant numbers of small lobsters have been reported in *Zostera* beds.

Habitat selection and mobility in adult lobsters

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Introduction

Whilst the European lobster (*Homarus gammarus*) is a familiar, large, commercially important species surprisingly little is known about its movement and behaviour (Cooper and Uzman, 1980). This review examines the habitat selection and movement of the clawed lobsters H. *gammarus* and *Homarus americanus*, the latter having been studied more intensively.

Habitat

Lobsters are usually associated with rocky substrates which afford shelter. Benthic habitat selection by all species of lobsters has been reviewed by Spanier (1994). Clawed lobsters, *Homarus*, are cryptic during early benthic stages. The behaviour of artificially reared *H. gammarus* yearlings has been described by van der Meeren (1993). After a few years of settlement, *Homarus.* emerge having reached a carapace length of 25-40mm (Wahle and Steneck, 1991). The driving forces for this change, nutritional requirement and outgrowing shelter, are discussed by Cobb and Wahle (1994). Adult *Homarus* are known to be solitary (Atema and Cobb, 1980). Wahle (1992a) describes a general pattern of diminishing predator avoidance with greater body size of *H. americanus*, although they continue to shelter as adults (Wahle, 1992b). Larger animals tend to reside less permanently in a given site (Karnofsky *et al.*, 1989a, b). Shelter availability is a critical feature of lobster habitat (Cobb, 1971; Karnofsky *et al.*, 1989a, b). Habitats are selected where burrows can be dug or exist under rocks or boulders (Stewart, 1972; Cooper and Uzman, 1980; Campbell, 1986). Auster *et al.* (1991) observed adult lobsters on the continental shelf at 55m in depressions excavated through a dense shell cover. Field studies by Cobb (1971) showed that *H. americanus* occupied shelters whose height was less than their width and that there was a correlation between lobster and shelter size. The excavation of sand and gravel to modify shelters was described in detail. Laboratory studies were carried out with various sizes and configurations of shelters. In field surveys Richards and Cobb (1986) found *H. americanus* and crabs (*Cancer borealis*) occupying a similar range of shelter sizes, though in laboratory experiments lobsters were competitively superior. Bologna & Steneck (1993) demonstrated the role of kelp beds in providing shelter for *H. americanus* by providing real and artificial kelp plots.

Dybern (1973) describes the relative frequency of habitat occupation by lobsters (*H. gammarus*) off the Swedish west coast. The highest frequencies were found in excavated burrows under boulders and stones on mixed sediment seabed and among or under boulders and stones on rocky seabeds. The shape of a typical burrow was found to be just high enough to permit the lobster to rise on its legs and take up a defensive position. The width of the opening was slightly greater than the height and the inside of the burrow often enlarged into a chamber. These may be extended to form a tunnel with one or more rear openings. A relationship between shelter hole size and lobster carapace length has been proposed by Cobb (1971), Wahle (1992b) and Barry & Wickens (1992). Wahle (1992b) presents a model of lobster-substratum scaling (fig. 1). As sediment particle size increases it provides interstices, shelters which can accommodate larger animals. Finer sediments

can be manipulated by animals, burrowing or moving material. Larger animals can move large particle size sediments.

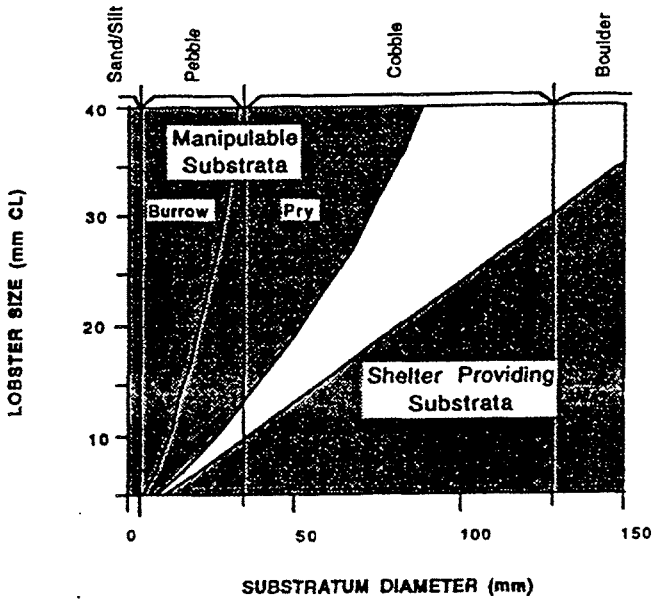

Figure 1 Model of lobster-substratum scaling (from Wahle, 1992b)
Figur 1 Modell for skalering av hummer substrat (fra Wahle, 1992b)

Stewart (1972) and Cobb (1971) suggested that a lack of natural shelter may limit the distribution of lobsters in inshore areas. The mean size of lobsters caught from the Norfolk coast of the UK has long been recognised as being smaller than those from other fisheries (Howard, 1980). Diving observations showed fewer large-scale outcrops and more boulders and cobbles than other sites. It is suggested that the lack of solid cover of suitable size limits the survival of larger animals. Observation of habitat limitation in some areas has led to the construction of experimental artificial reefs to extend the availability of suitable shelter. Scarratt (1968, 1973) studying a quarried rock reef, found a lobster (*H. americanus*) biomass equal to or greater than that of nearby natural productive ground. Using pumice concrete shelters, Sheehy (1976) found similar results. Colonisation of a concrete block artificial reef by *H. gammarus* in the UK has been described by Collins *et al.* (1991, 1992, 1993, 1994) and Jensen *et al.* (1994). A simple model to estimate the number and sizes of crevices visible at the surface at the surface of an artificial spherical rock reef intended to provide shelter for lobsters and crayfish has been produced by Barry & Wickins (1992).

Movement

Work on *H. gammarus* movements, by Thomas (1954) off the Scottish coast and Simpson (1961) off Wales showed that the majority of animals studied moved only small distances, averaging 3.2 km and 1.4 km respectively. Simpson (1961) recorded a maximum distance of 10 km between original capture and recapture locations.

Much of the recent work in the UK has concentrated on lobster stock enhancement experiments by the Ministry of Agriculture, Fisheries and Food.During the past 10 years hatchery-reared juvenile lobsters have been released at several sites around the UK. Large numbers of the micro-tagged hatchery-reared animals have subsequently appeared in commercial catches. Off the north-east

coast of the UK, the distance between juvenile release site and adult capture location was generally less than 3 km (Bannister *et al.*, 1994).

The American lobster, *H. americanus*, has been much more intensively studied (Campbell, 1989; Campbell & Stasko, 1989; Duggan, 1991; Fogarty *et al.*, 1980; Krouse, 1981; Maynard, 1991; Miller *et al.*, 1989). Inshore *H. americanus* smaller than 100mm carapace length (CL) were shown to move locally with dispersals often below 300 m from their home shelters: a small proportion of these lobsters were found to have moved up to 2 km (Cooper and Uzmann, 1977; Lund and Rathburn, 1973). Limited movements within the American lobsters' home range have been suggested to be night time food-foraging excursions, mainly taking place in warmer summer and autumn waters, and are usually followed by a return to the same or a nearby shelter (Stewart, 1972; Cooper and Uzman, 1980). Additional short-distance movements were recorded for inshore *H. americanus* during storms and heavy seas from shallow (5-20 m) to deeper waters (30-60 m). Extensive onshore-offshore migrations have been recorded for large (>100 mm CL) *H. americanus* (Cooper and Uzmann, 1980; Dow, 1974), although no such behaviour has been observed for the European lobster (Cooper and Uzmann, 1980).

Poole Bay, UK studies

Poole Bay, on the central south coast of the UK has a silty-sand seabed with small rocky reefs, which are fished commercially for lobsters, and crabs (*Cancer pagurus*). In 1989, a small experimental artificial reef was deployed in western Poole Bay on a flat, sandy seabed some 3km from the nearest rocky habitat (fig 2).

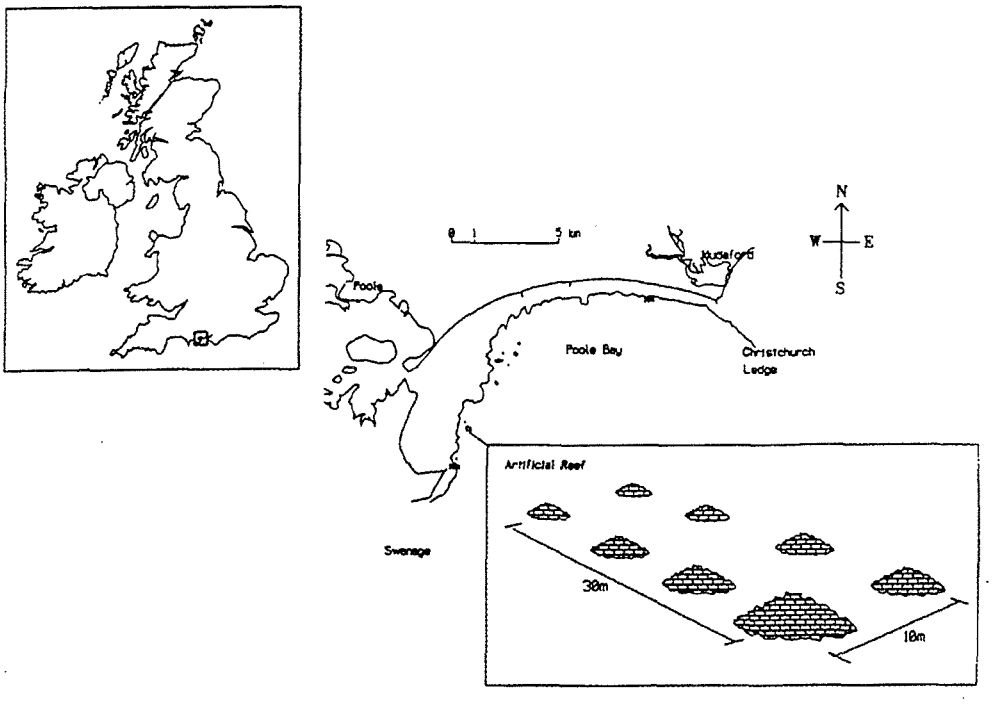

Figure 2 Location of the artificial reef in Poole Bay, England. (Jensen *et.al.*, 1994)
Figur 2 *Plassering av det kunstige revet i Poole Bay, England (Jensen et.al., 1994)*

Three weeks after deployment, and before epibiotic colonisation became established, research divers observed lobsters (*H. gammarus*) within the reef structures. This observation gave rise to speculation about the distances travelled by lobsters between areas of suitable substrata. In 1990 movement studies were initiated using conventional tagging of animals on the artificial reef and the commercial fishery to the north of the reef site. In 1992 and 1993, the tagging studies were extended to the adjacent commercial fisheries; Christchurch Ledge to the east and Swanage to the south. A total of 3500 animals have been tagged.

The artificial reef provides a well-defined environment in which to study unconfined animals. Between 1990 and 1993 151 lobsters were tagged on the artificial reef, 78 of which (29 male and 39 female) were recaptured at least once within the first year of release, with an overall first recapture rate of 52%. A lobster has now been observed on the reef during a period of 1050 days (a female; 12/8/90 to 29/6/93) and 17 others for periods of more than a year, demonstrating the suitability of the reef as a habitat for lobsters. In 1991, movements of two lobsters around the artificial reef were followed using acoustic pingers attached to the animals (Collins *et al.*, 1992). An electromagnetic tracking system was used in 1993 to track four lobsters continuously for two months (Collins *et al.*, 1994). Most activity occurred at night, starting soon after sunset and finishing before sunrise. A period of storms led to a cessation of activity followed by a period of low light intensity when a number of daytime movements occurred. Most movements were between reef units (Collins *et al.*, 1993), in the form of night-time excursions from a 'home/base' reef unit to visit one or more others before returning. The actual sequence of visits was often repeated on subsequent nights though an animal might change its base reef.

Lobsters also made excursions generally lasting 1-4 hours, away from the reef (Fig. 3) Most movements were within two hours of slack water, suggesting some preference for times of lower water velocity. One lobster left the reef for periods of 3.5, 7 and 21 days. Conventionally tagged animals moved away from the reef and were caught on natural reefs in the commercial fishery. Minimum estimates (since the directness of the route and actual departure and arrival dates are not known) of movement rates show figures in excess of 100 md^{-1} and one of 500 md^{-1}.

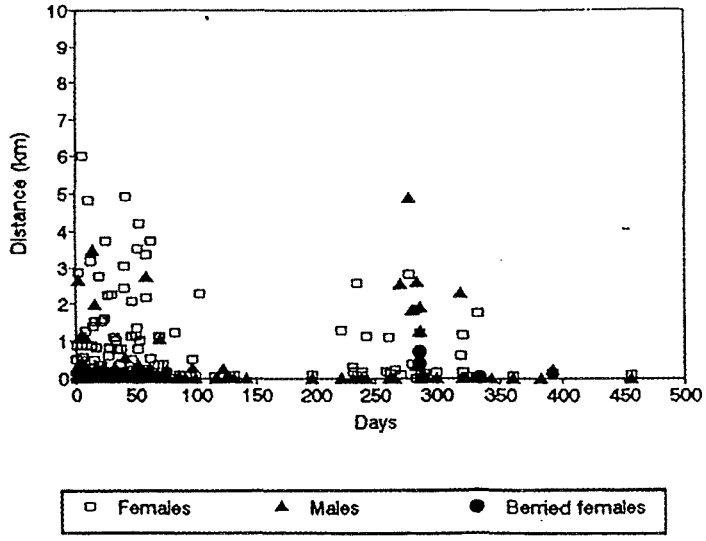

Figure 3 Lobster movement in Poole Bay. (Source Collins *et.al.*, 1992 C.M. 1992/K:42)
Figur 3 Hummerbevegelser i Pool Bay. (Collins et.al., 1992 C.M. 1992/K:42)

Twenty-one percent of 2000 lobsters tagged in Poole Bay were recaptured within 100 m of their original capture location (Jensen *et al.*, 1993). The majority of lobsters moved small distances (<2 km) from their initial capture location over periods up to two years, although a small number of individuals were recaptured up to 18.5 km from their release site. In general movement appears to be closely aligned with longshore tidal currents. Very little interchange of lobsters has been observed between the Poole Bay fishery and the adjacent fisheries 5-10 km distant.

Reasons for movement

Naylor (1988) has described the locomotor behaviour of decapod crustacea, in phase with dial, tidal and other rhythms. Evidence for nocturnal movement of both American and European lobsters has been reviewed by Cooper and Uzman (1980) who noted that there were no published data on the timing of excursions by *H. gammarus*. This species has been observed foraging for food at night (Hallbäck and Warren, 1972; Dybern, 1973; Berril, 1974). Dybern (1973) also observed that lobsters will leave their shelters for food during the day in low light intensity during periods of poor underwater visibility.

Weiss (1970), studying *H. americanus*, noted increased activity within burrows one to two hours before sunset. Within an hour of sunset, in July, 10% of animals were observed to have left their shelters, and 80-90% four to five hours after darkness. A light intensity of less than 2×10^{-2} TW cm (during June to November) was found to be the trigger for movement out of, and return to the burrow/shelter. This light intensity threshold was found to be lower, 0.2×10^{-2} TW cm^2 during January and February, presumably in responds to the lower ambient light intensities at this time of year. Ennis (1984) recorded peak activities two to three hours after darkness. Cooper and Uzmann (1980) suggest that activity levels were determined by a combination of daylight, water clarity and the amount of light reaching the sea surface. From the Poole Bay artificial reef study, another factor, water movement (tidal and storm swell induced) could be added to this list.

The majority of short (<4 hrs) excursions from the Poole Bay artificial reef were close to slack water, the time of least hydrodynamic drag on the animal. A flume study of lobster reactions to current speed (Howard and Nunny, 1983) showed that movement with or against the current was limited at velocities above 0.1 m s^{-1} and ceased above 0.2 m s^{-1}. Another study by Howard (1988), off the Norfolk coast, indicates concentration of activity around periods of slack water. Baited plates were photographed with a time laps camera through several tidal cycles.

Excursions from the reef could be considered as exploration/foraging trips around the reef. One destination has been the historic wreck site 100 m south of the reef. Pots placed 10 and 20 m away from the reef caught only one animal, which does not suggest much off-reef activity. However during the electromagnetic tracking experiment only one out of four animals was caught in the course of two months, indicating that trap capture does not necessarily reflect animal activity. The longer duration movements (up to 21 days) suggest that more distant sites were visited, possibly the natural rocky habitat three km away. Providing information on the longer-term movements of lobsters, these data show that the majority of lobsters moved small distances (<2 km) from their initial capture location over periods of up to two years. The lack of interchange between the Poole Bay and adjacent fisheries is similar to the results obtained from studies of *H. americanus* by

Stasko (1980). Newfoundland lobsters in shallow waters of large bays were not found to migrate from one bay to the next, nor was summer inshore to winter offshore migration by adults observed, in contrast to the behaviour observed in other areas (Dow, 1974). This type of migration may take energetic advantage of different water temperatures, but in the Newfoundland bays studied by Stasko (1980) there are no large temperature differences between summer and winter.

There is evidence for navigation, on the scale of metres, around the artificial reef and on the scale of 100m to kilometres, through excursions from the artificial reef and between natural reefs in Poole Bay. Direct observation of lobster movement between artificial reef units suggests that they are aware of the location of neighbouring units and can navigate accurately. The distances are greater than underwater visibility, indicating the use of other senses or mechanisms to aid navigation. The use of chemoreceptors by *H. americanus* to locate food has been described by Derby and Atema (1982). Chemical signals in urine play an important role in the mating behaviour of this species (Bushmann and Atema, 1993). Many movements on the artificial reef were across or down current, suggesting that scent clues were not the primary means of navigation. Lohmann (1984) has shown the retention of magnetisation by tissues of the Atlantic spiny lobster, *Panulirus argus*. The study showed concentration of ferromagnetic material in the cephalothorax with different orientations of remnant magnetisation on different sides of the body. It was suggested that this could result from the ordered alignment of permanently magnetised particles comprising a magnetoreceptor system. The ability of this species to use the earth's magnetic field was shown in circular chamber experiments by Lohmann (1985).

Behaviour studies using telemetry

Acoustic (ultrasonic) methods have been widely used for marine telemetry (Stasko and Pincock, 1977; Pincock and Church, 1984). Ultrasonic pingers were used to mark lobsters *(H. gammarus)* on an artificial reef which have been tracked with a directional receiver from the surface or accurately located underwater by divers using an omnidirectional hydrophone probe inserted between reef blocks (Collins *et al.*, 1992). The manual tracking of berried female H. americanus in Jeddore Harbour, Canada has been described by Jarvis (1990). This approach has been developed further by using an array of buoys equipped with ultrasonic receiver and radio transmitter (O'Dor and Webber, 1991; Duggan *et al.*, 1991). Four berried lobsters were tracked for five days over an area of four km^2, moving distances from 1.5 - 15 km. However when animals are resident within reefs rather than free-ranging over open seabed, the effectiveness of acoustic methods is limited by reflections from rock surfaces and signal attenuation when the lobsters were within passages in the reef. Automated acoustic tracking systems compute the position from the measured times for the pinger sound pulses to reach three or more receiver stations. If the paths are not straight, i.e. are reflected off rocks, then the result is incorrect. The application of electromagnetic propagation through rock for mine communications has been described by Austin (1987). Propagation through seawater was investigated by Dunbar (1972). The achievable range of electromagnetic/inductive coupling in seawater is low compared to acoustic methods but it is not severely attenuated by rock, concrete or seawater.

One of the earliest examples of its application to animal telemetry was described by Mackay (1964) who used low-frequency radio to transmit body temperatures of marine iguanas in the Galapagos. Ramm (1980) first described the application of electromagnetic telemetry in Australia to track rock lobster (*Jasus novaehollandiae*) movements around shallow inshore reefs. The signals from transmitting tags on lobsters were detected by aerials laid out in a grid on the seabed and linked to a shore-based receiver. Using the same tag and with developments in the aerial array and receiver the system was used to study another species (*Panulirus cygnus*), Phillips *et al.* (1984); Jernakoff

(1987a, 1987b); Jernakoff *et al.* (1987); Jernakoff and Phillips (1988). The methods described by Ramm (1980) have been developed further (Collins *et al.*, 1994) for tracking lobsters (*H. gammarus*) on an artificial reef. Long-term (one year) tracking of large numbers (>20) of lobsters on the artificial reef is planned to examine the correlation of behaviour with physical conditions (Collins, 1995). Two further developments are foreseen; a) the incorporation of physiological data (heart beat, muscle activity) in the tag transmission and b) the addition of an acoustic component to enable long-distance tracking during excursions away from the reef.

The limited range is of less importance in laboratory experiments. Graham (1981) describes the development of an electromagnetic tag for monitoring crab heart rate. The application to fish has been described by Priede *et al.* (1984). Breukelaar *et al.* (1995) are developing a transponding electromagnetic tag for tracking the migration of sea trout (*Salmo trutta trutta*) in the Netherlands. Antenna loops will be laid across riverbeds.

Conclusions

Conventional external visual tagging and, more recently, micro-wire tags for juveniles have been used to provide information about the extent of movements in lobster populations. Mark/recapture studies also provide information about stock density, currently assuming that all animals will enter traps. These tagging studies are relatively long-term with days, weeks or even years between capture events. Thus these are unlikely to yield information about the underlying reasons for behaviour. Acoustic tracking has been successfully used to monitor movements of lobsters over a scale of kilometres. On a small scale the electromagnetic tracking of resident lobsters on the Poole Bay artificial reef has provided detailed information about the timing of movements, enabling these to be related to light intensity, tidal and storm swell-induced water movements. The long-term extension, beyond one year, of this study will reveal seasonal factors. Continuous monitoring of large numbers of animals in a small area will not only increase confidence in the data but may reveal animal interactions. Incorporation of physiological parameters into telemetry studies will offer greater insight into the mechanisms of lobster behaviour. Information about the utilisation of habitat and movement of animals contributes to an understanding of the stock density of the species and its catchability, both of which are vital components of fishery management models.

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Habitat selection and mobility in adult lobsters

Discussions

In Europe adolescent and adult lobsters are found predominantly on rocky ground (bed rock, boulder, or cobble), but also in cohesive mud or in hollows. Adults continue to use shelters as protection during moulting and mating, against predation, and to help cope with water movement.

Habitat size and type can affect the carrying capacity of an area and may influence the size composition of lobsters in the area.

Even where there appears to be adequate shelter, tagging has shown that lobsters may migrate. Studies in Norway and in other parts of Europe point to these movements generally being small (less than 5 km) and not in any particular direction. However, there are inshore-offshore movements reported in some areas and there is the possibility of some contra current movement.

At the local level, foraging movements and seasonal, tidal, and diurnal movements will influence the frequency of encounter by lobsters with baited traps. Electromagnetic tracking of lobsters can provide detailed information on this important aspect and can lead to better modelling of the capture process.

The conclusion is that more need to be known about where and why lobsters stay or move in and between habitats. It is today no knowledge the lobsters movements in the sea.

Information on dispersal of each life-history stage will assist fishery modelling and help in determining stock structure. The significance and source of large lobsters offshore of Norway is unknown.

The assessment and population dynamics of the European lobster, *Homarus gammarus* (L.).

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Background

The total landings of *Homarus americanus* on the American and Canadian east coast are in the range of 40 000 to 80 000 tonnes per annum. By comparison the stocks and fisheries for *Homarus gammarus* are very small: officially recorded European landings (1945 to 1990) averaged 2370 tonnes. Many of these may well be significantly under-recorded or under-reported, but are still an order of magnitude less than for *H. americanus*, reflecting a major difference in the extent and abundance of the stocks of the two species.

This contribution is presented from an UK perspective.

Distribution and stock structure

Lobsters are extensively distributed at moderate abundance round most UK coasts wherever the habitat provides suitable shelter, mainly cobbles, boulders and bedrock. Traditional fisheries occur within 12 miles of the coast, but fisheries a few miles further offshore have developed during the past decade, e.g. near-coast wrecks and oil platforms.

Extensive results from tagging both natural and hatchery reared stock show that in English and Welsh waters, a small proportion of individuals migrates along the coast for distances of up to 20 km or more, but that most lobsters only move locally, within embayments. This contrasts with the marked migration of female *Cancer pagurus* (Bennett & Brown, 1983) and the extensive migrations of *H. americanus* to (autumn) and from (spring) deeper, and warmer, water (e.g. Pezzack, 1987).

In some localities, such as Bridlington Bay on the east coast of England, the hydrographic regime suggests that lobster larvae may be transported offshore at the surface, then returned inshore nearer the sea bed, prior to the active settlement stage. In general, lobster larvae are hard to find. Neuston net surveys on the English east coast found lobsters larvae to be sparse and low in number (Nichols and Lovewell, 1987), with the result that their distribution and settlement have not been studied systematically. Juveniles smaller than the smallest size retained in lobster traps (about 50 mm CL) have not been readily found or observed by divers. The biological links between spawners and recruits are therefore not well established, and individual stock boundaries are not readily identifiable. Management units have therefore been chosen to coincide with the operational area of the fisheries rather than on a strict biological basis.

The fisheries

Most UK fisheries correspond to a 10-20 mile stretch of coastline, fished by 10 to 20 full-time lobstermen and numerous part-time or hobby fishermen. A typical season runs for about 150 fishing days a year between March and October. Lobsters are mainly caught using creels, parlour pots or inkwell pots, generally fished in fleets of 20, 25, 30, 50 or 80 , depending on the locality and the depth. Part-time men use 20 to 100 pots, and full time men 250 to 1200 pots. Most are hauled four or five times a week, but the larger pot numbers are usually hauled less frequently. Legal size is 85 mm carapace length, and the average animal caught weighs 0.5 to 1 kg. Average daily catch rates vary from 10 to 15 lobsters per 100 pot hauls in poor fisheries, up to 40 to 80 lobsters per 100 pot hauls in the better fisheries.

Landings

Post-war lobster landings in England and Wales have fluctuated between 300 and 600 tonnes. From 1955 to 1980, there was a prolonged decline, since followed by a progressive rise (Figure 1). The decline was most notable along the north east and west coasts, while the recent increase has been most notable in Yorkshire, Norfolk and the Channel.

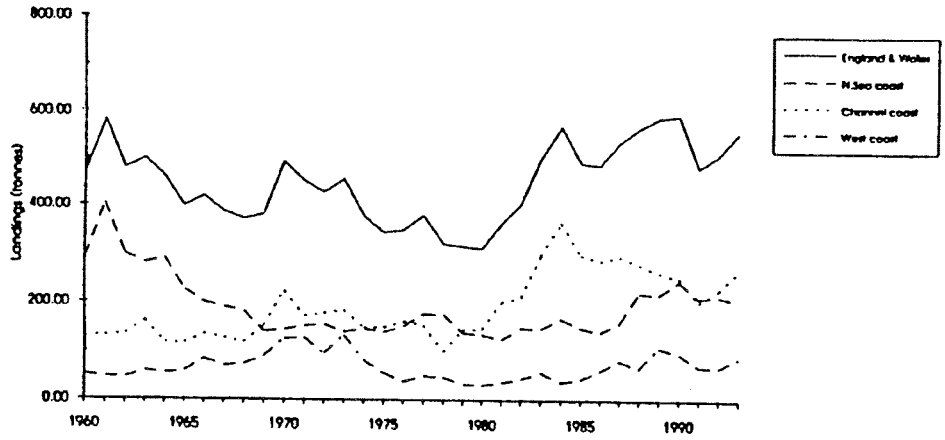

Figure 1a Trend in landing of the European lobster round the coast of England and Wales. (Source: MAFF Offical Statistics)

Figur 1a Utvikling av hummerleveranser rundt kysten av England og Wales. (Kilde: MAFF Offical Statistics)

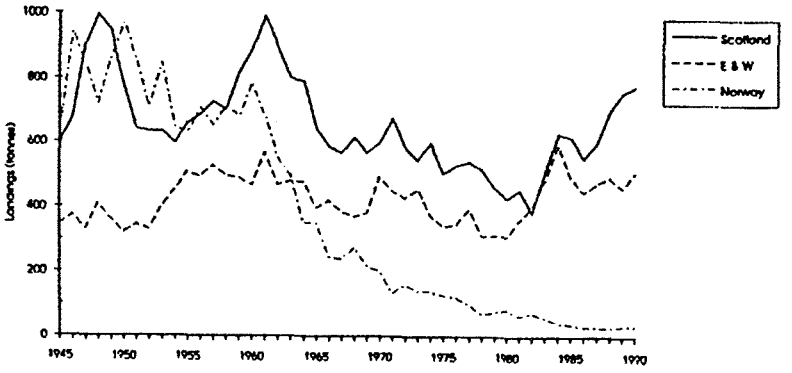

Figure 1b Trend in landing of the European lobster in Scotland, England & Wales and Norway . (Source: MAFF Offical Statistics)

Figur 1b Utvikling av hummerleveranser i Skottland, England and Wales og Norge. (Kilde: MAFF Offical Statistics)

General modelling for assessment and management

Lobster assessments are usually made using size distribution data obtained by sampling the landed catch on the quayside (legal size only), or sampling the total pot content caught at sea prior to discarding undersized animals.

Size distribution is a function of underlying growth and mortality schedules, modified by any limiting effect of shelter size selection at capture due to pot size and design.

Growth

Moulting makes it difficult to study lobster growth directly and accurately. Most lobster growth equations are calculated from Walford plots of average post- and pre-moult size (L_{t+1} against L_t) obtained one year apart using conventional tagging data. The intercept on the 45 ° line is L oo, and the growth constant (k) can be estimated from the slope, or the intercept. The grouping of returns in annual time intervals, and by incremental groups, allows moult frequency to be taken into account, but because tag- recapture data tend to be for a rather limited size range (85 to 120 mm CL at most), the resulting growth equations are almost certainly unrepresentative of the true growth of larger animals. Nevertheless, new data from the recapture of hatchery-reared lobsters released during recent UK stock enhancement experiments provide convincing corroboration of the long-held assumption that lobsters in UK waters require four to six years to reach the 85 mm CL legal size (see Figure 2, from Bannister *et al.*, 1994).

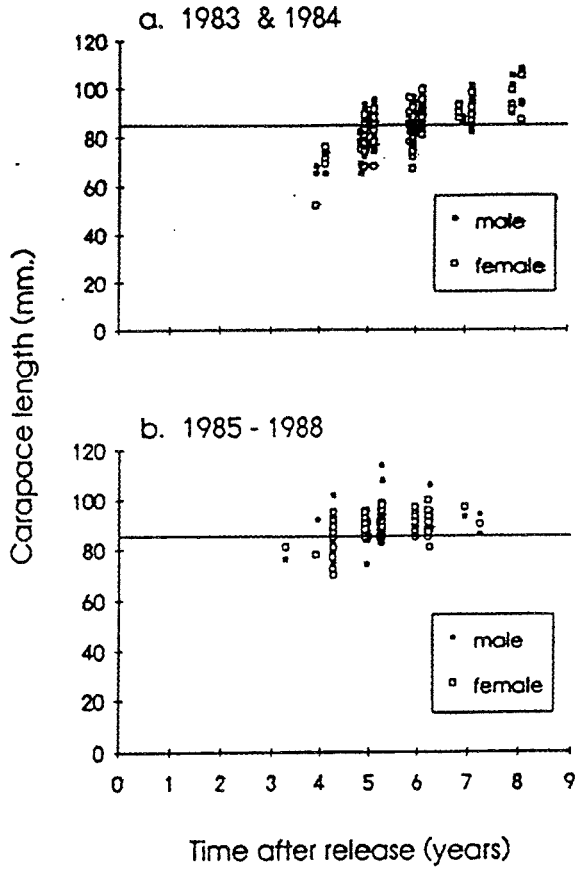

Figure 2 The size at recapture of hatchery-reared European lobsters released as juveniles in Bridlington Bay, England in a) 1983 & 1984; b) 1985-88 (Source: RCA Bannister, JT Addison and SR Lovewell, MAFF Fisheries Laboratory, Lowestoft, UK).

Figur 2 Størrelse på gjenfanget hummer satt ut i Bridlington Bay, England i årene; a) 1983-84; b) 1985-88. (Kilde: RCA Bannister, JT Addison and SR Lovewell, MAFF Fisheries Laboratory, Lowestoft, UK).

Mortality

Mortality is estimated using length cohort analysis (Jones, 1981). The method estimates the rate of change of numbers during the time interval required to grow from the lower to the upper limit of a size class. This time is calculated as an average for all lobsters, based on the von Bertalanffy growth equation. The most commonly used class in 5 mm, which is less than an annual increment. At the lower end of a growth curve, lobsters grow through one or more size classes a year, and a size class may be predominantly one cohort. At the upper end, near to L oo, it takes increasing by longer to grow through a size class as moult frequency declines, and so there are more cohorts per size class. Thus, equal size intervals do not correspond to equal time intervals, and size and time intervals do not correspond to cohorts. The rate of mortality calculated for each size interval must be raised to an annual value, and except at the lower end of the size distribution it is unlikely to represent the mortality of an individual cohort.

Yield per recruit and minimum size calculations

When length cohort analysis is used to assess the effects of changing effort or minimum size of first capture, the length-age problem in crustaceans is circumvented. For a specified multiple of current effort, the method simulates change by multiplying the present size class affected by any change in minimum size composition in the same proportion. It also redistributes the animals in the size class affected by any change in minimum size. The resulting yield and stock biomass per recruit are expressed as corresponding ratios of the present value (Jones, 1981). This is an equilibrium steady-state approach.

The underlying rationale is the same as for an age-structured model, in that when fishing mortality is high the size distribution is expected to comprise lobsters mainly in the size groups just above minimum size, whereas when mortality is low the size distribution includes many animals in the larger size class (Figure 3a, from Addison, 1986). Consequently the change in biomass and yield per recruit reflect the effects of allowing lobsters to survive and grow to large size, or not, as the case may be.

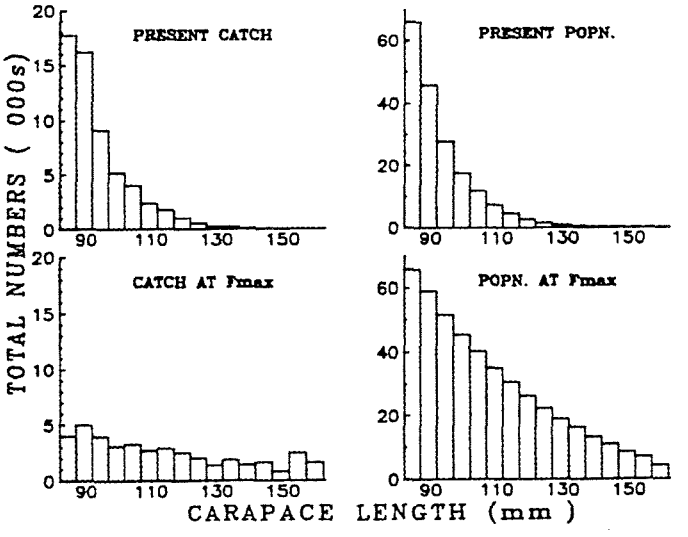

Figure 3a Size composition of the lobster catch and stock at high effort, and at F max (reduced effort). (Source: JT Addison, MAFF Fisheries Laboratory, Lowestoft, UK)

Figur 3a *Størrelse fordeling i hummerfangster og bestand ved høy fangst innsats, og ved F max (redusert innsats) (JT Addison, MAFF Fisheries Laboratory, Lowestoft, UK)*

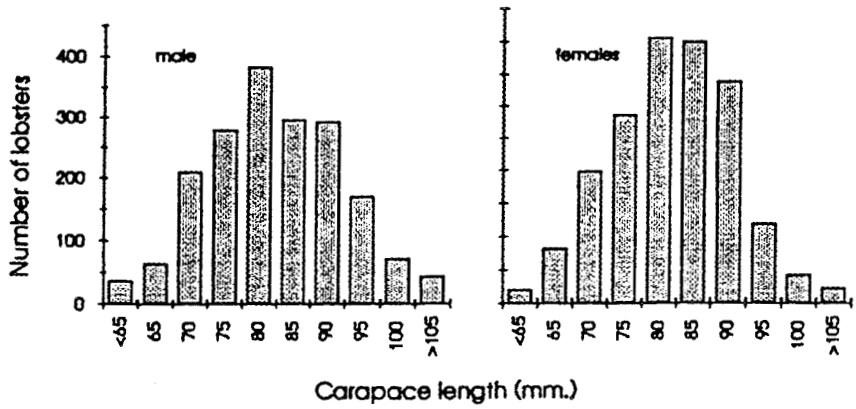

Figure 3b Size composition of landings from a typical English east coast fishery. (Source: JT Addison, RCA Bannister and SR Lovewell, MAFF Fisheries Laboratory, Lowestoft, UK.)

Figur 3b *Størrelse fordeling i hummerleveranser fra et typisk engelsk østkystfiskeri. (Kilde: JT Addison, RCA Bannister and SR Lovewell, MAFF Fisheries Laboratory, Lowestoft, UK.)*

Figure 3b shows the size distribution from a typical heavily exploited stock, and Figure 4 illustrates yield per recruit and biomass per recruit curves for different minimum sizes for different fisheries in England and Wales (Bannister, 1986). These allow us to examine the cost-benefit trade-offs between raising minimum size, or reducing F, or both.

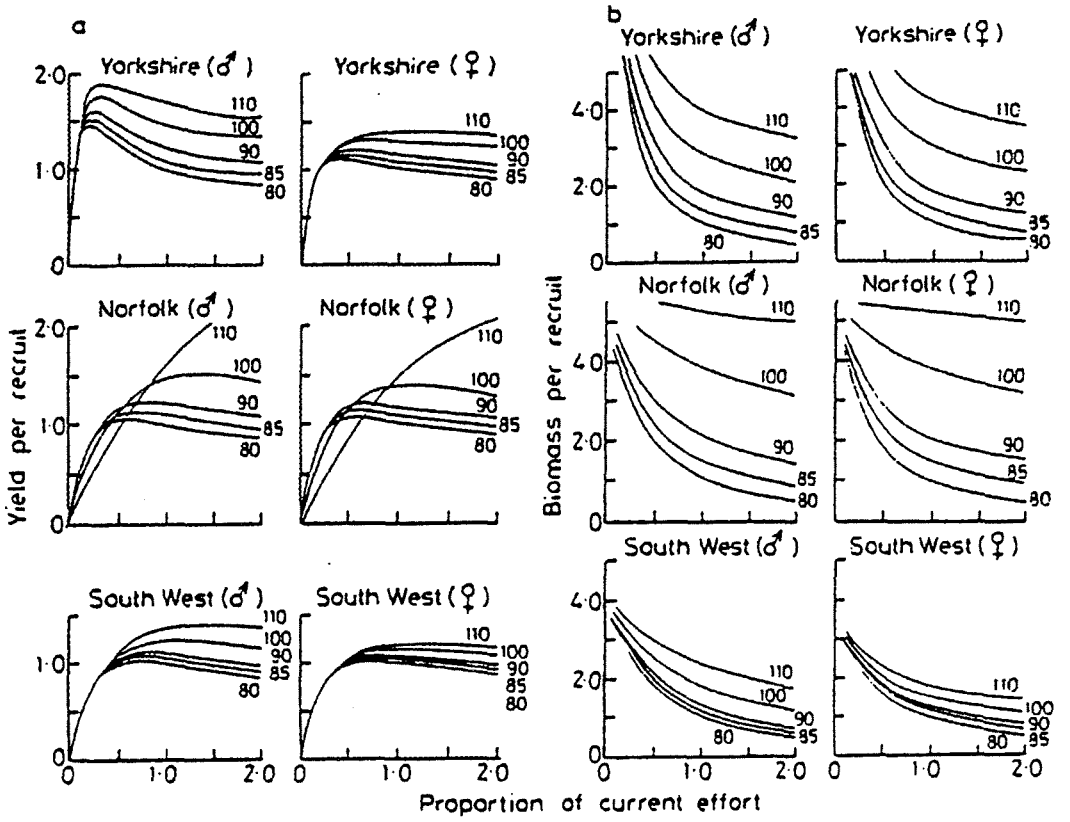

Figure 4 Curves of a) yield per recruit and b) biomass per recruit against fishing effort, for various minimum sizes, for the European lobster in coastal waters of England and Wales. (Source: RCA Bannister, et.al., MAFF Fisheries Laboratory, Lowestoft UK)

Figur 4 Kurver som viser a) avkastning pr. rekrutt og b) biomasse pr. rekrutt mot fiskeinnsats ved ulike minste mål, for hummer i England og Wales. (Kilde: : RCA Bannister et.al., MAFF Fisheries Laboratory, Lowestoft UK)

Limitations of the simple model

Length cohort analysis uses size distribution as a catch curve, so that mortality across length groups (and hence across cohorts) is only unbiased in a steady state, with no trends in recruitment and/or mortality to influence the relative abundance of each cohort. Size distributions are usually averaged over several years to minimise the possibility of bias.

In fact, it is often the case that lobster size compositions appear to change very little with time. This is less likely to reflect a steady state condition (since it often occurs even when fishing effort is changing) than the possible effect of three different ancillary factors, with very different implications. Firstly, fishing mortality may not be linearly related to fishing effort, which might be the case if lobster density is low, and effort saturation occurs at high trap density. In this case, the size distribution may be realistic, and the estimated mortality unbiased, albeit uncorrelated with fishing effort. Secondly, the size distribution derived from sampling traps could be heavily biased by selectivity at both the lower (escapes) and upper (reduced entry of large lobsters) ends of the size range. Observed size distribution could then underestimate the number of older lobsters in the stock, but not necessarily the catch. Thirdly,

large lobsters might show density-dependent mortality due to habitat limitation. In this case, size composition may be accurate, but will underestimate total mortality, mask potential trends in mortality as effort increases, and overestimate the benefit of increasing minimum size, as modelled in some detail by Addison (1986).

Some evidence that habitat might influence size distribution was put forward by Howard (1980), while the combined effect of trap design, pot selectivity and habitat were investigated in the field by Addison and Lovewell (1991) using comparative fishing experiments.

Stocks and recruitment

Although many ecological processes are size-dependent, length-based analysis is deficient for studying recruitment, which is year-dependent. The use of size distribution as a catch curve, the lack of correspondence between length classes and individual cohorts, and the averaging of data across several years, mean that cohort analysis output does not identify individual cohort data, and cannot be use to make stock-recruit plots. This cannot be remedied until a cheap and reliable age determination tool becomes available for routine ageing of large numbers of lobsters in the field. Using length cohort analysis output on a per recruit basis obviously underestimates the likelihood of stock collapse at high effort levels, as has been simulated in detail by Bannister and Addison (1986) for several different types of assumed stock-recruit relationship (Figure 5).

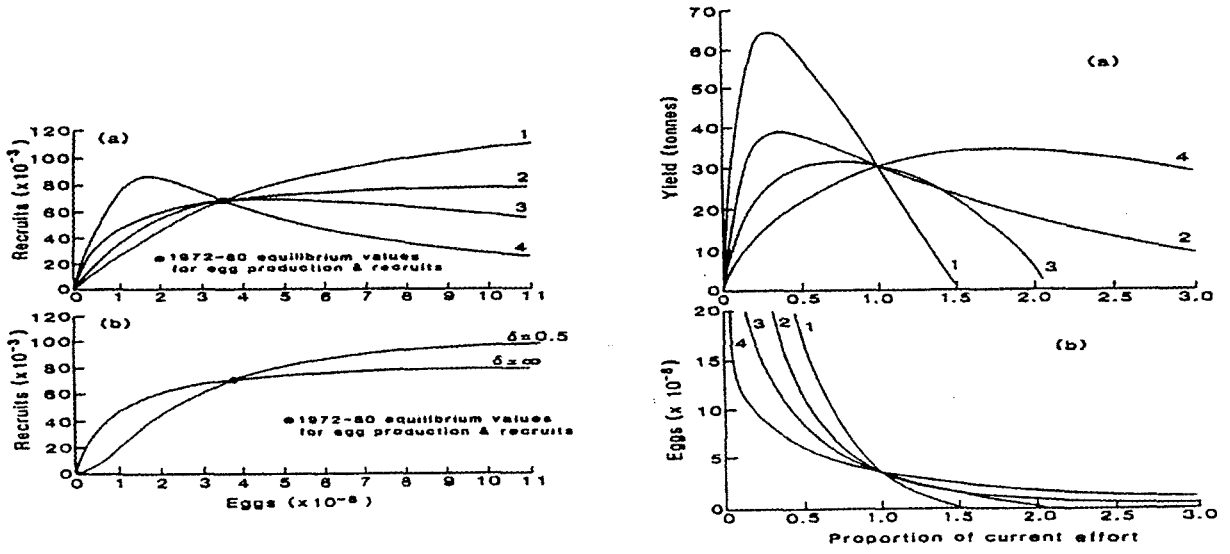

Figure 5 Simulated stock and recruitment curves, and corresponding yield-effort curves for the European lobster in England and Wales. (Source: RCA Bannister and JT Addison, MAFF Fisheries Laboratory, Lowestoft, UK).

Figur 5 Simulert bestand og rekrutteringskurver, med korresponderende avkastning pr. innsats kurver for hummer i England og Wales. (Kilde: RCA Bannister and JT Addison, MAFF fisheries Laboratory, Lowestoft, UK).

Under the various assumptions about stock and recruitment made by Bannister and Addison (1986), the fishing mortality predicted to optimise total yield is less dependent on the assumed value of natural mortality than for a yield per recruit model. Although the coefficient of natural mortality (M) has not been measured specifically in *H. gammarus*, it is customary to assume that M=0.1, on the grounds that adult lobsters are shelter seeking, have few predators, and probably survive moulting well. It is sometimes suspected, however, that occasional pulses of high natural mortality may occur in winter, when substantial numbers of dead lobsters are washed ashore following prolonged onshore winds and heavy wave action in shallow water. Such intermittent catastrophic effects are not normally taken into account in the traditional assessments.

Stock and recruitment has been studied for *H. americanus* using series data for the Northumberland Strait stock in Canada (Fogarty and Idoine, 1986). Abundance of the four successive planktonic stages of larvae were well correlated, and showed no sign of compensatory mortality. In contrast the relation between adult stock and larvae stage IV was markedly asymptotic, showing that compensatory mortality must have occurred between settlement and recruitment to the fishery five years later. The bottleneck was not identified, although habitat carrying capacity is an obvious candidate. In *H. gammarus* preliminary analysis of data for the recapture, as adults, of hatchery-reared lobsters released at three

months of age (post-settlement) suggests that survival during the four-year early benthic and adolescent pre-recruit stages was on the order of 50% (Bannister, Addison and Lovewell 1994). Adult abundance pre- and post- recruitment at 85 mm CL is also strongly correlated without signs of density dependence (Addison *et al.*, 1995). These results suggest that if carrying capacity does cause density dependent mortality, it is most likely to occur at the settlement stage itself, although, in *H. gammarus*, larval density, and hence presumably settlement density, was very low on the few occasions when it has been measured (e.g. Nichols and Lovewell, 1987).

Assessment Results

Bannister and Addison (1984), as reported in Bannister (1986), used coastal size composition data and growth equations derived from tagging to calculate fishing mortality and yield per recruit curves for several coastal areas of England and Wales. The annual coefficient of fishing mortality mostly varied from 0.2 to 0.9, but was 1.6 for an east coast area (Norfolk) where small lobsters predominate. The size composition in Norfolk is considered to be influenced by substrate (Howard, 1980). These results suggest that a large reduction in fishing mortality would be required to optimise yield per recruit, and a similar result was obtained for south-east Scotland by Shelton *et al.* (1978). The biomass per recruit curves show that the major change in biomass, and hence population egg production, occurs at a relatively low fishing mortality, which is likely to have been some time well in the past in most long-established fisheries.

Taking the underlying size composition data at face value, the simulation study by Bannister and Addison (1986) indicates that effort would need to fall by as much as 75% in order to optimise total yield, assuming that the stock-recruit curve is asymptotic. Lobster populations therefore appear to be suffering markedly from growth overfishing. There are obvious ground for concern about the possibility of future recruitment failure if fishing effort is maintained at its current level, or increases even further.

The yield per recruit curves in Figure 4 are very similar in shape to those derived by Fogarty (1980) for coastal stocks of *H. americanus* in the USA, implying that there is a marked similarity in the underlying growth and size distribution data for the two species and their fisheries. Fishing mortality values calculated for the USA stocks in the 1970s (Anthony, 1980) were even higher than those mentioned above for *H. gammarus*, and very large reduction in effort would seem to be required to optimise yield per recruit in the USA. Despite this, lobster recruitment did not appear to decline, perhaps because of recruitment from less heavily exploited offshore stocks. Indeed, after the mid- to late 1980s, landings of *H. americanus* in almost every part of the north eastern seaboard suddenly rose very substantially, to an all-time high in some cases. As there was no change in the management regime, it has been questioned whether this unexpected trend followed a widespread environmental change, or a recruitment-led increase in fishing effort, or factors associated with recruitment bottlenecks (see for example Addison and Fogarty, 1992). The question is unresolved, but the event exposes the limitation of perceptions based on simple assessment techniques which do not embrace a detailed underlying understanding of individual life history and of the local and regional ecology (see Figure 6 a summary of the relevant life history and fishery factors).

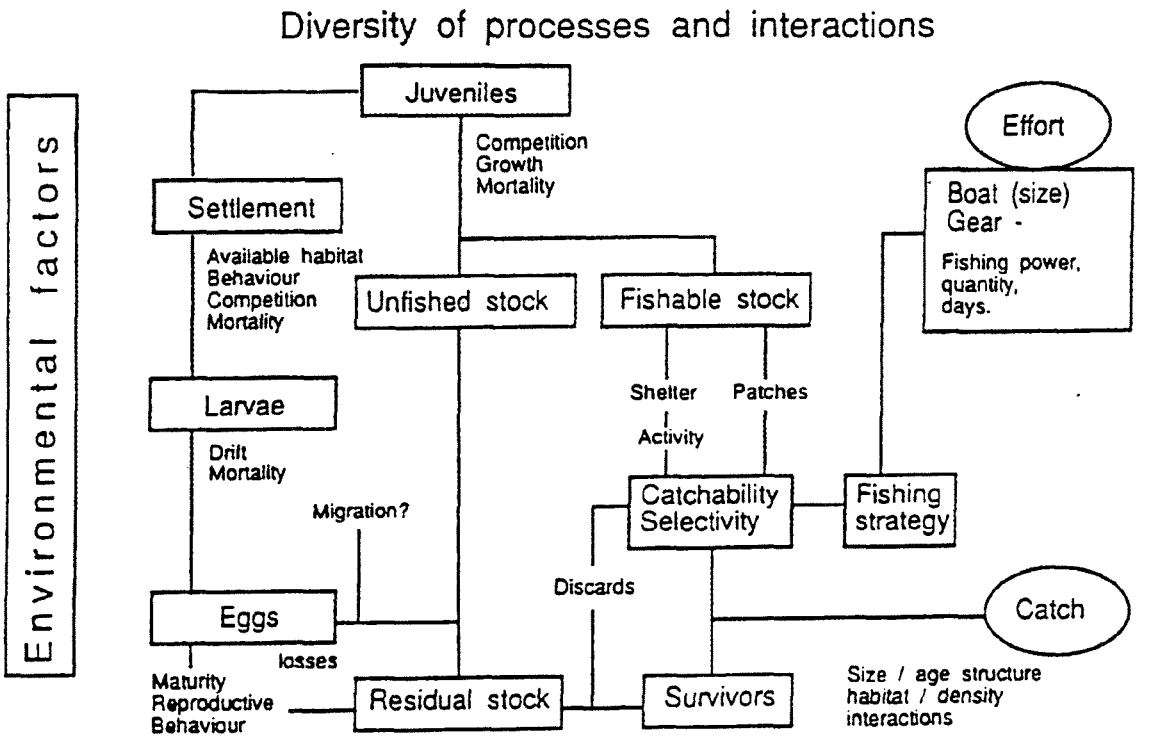

Figure 6 Schematic diagram showing the life cycle of the European lobster, and its interaction with the lobster fishery. (Source: RCA Bannister, MAFF Fisheries Laboratory, Lowestoft, UK).

Figur 6 *Skjematisk oversikt over livssyklusen til Europeisk hummer, og hvordan den påvirkes av fisheri. (Kilde: RCA Bannister, MAFF Fisheries Laboratory, Lowestoft, UK).*

The point is emphasised by the *H. gammarus* population in the Norwegian Skagerak, where, following relatively high landings pre-war when effort was also high, catch per effort and landings declined progressively from 1950 to a very low level in the 1980s (Tveite and Rørvik, 1982). Fishing effort also declined, and this, combined with the very low stocks, clearly suggest that the recruitment had failed, but whether as a result of previous overfishing, or some concurrent environmental factor, is not clear. The decline in lobster stocks was accompanied by an increase in the abundance of *C. pagurus*, but it was not clear wether the change in crab abundance caused, or followed, the change in lobster abundance (Tveite, 1979). Coincidentally, lobster landings in Scotland and the north east of England also decline progressively from 1960 to 1980 (Figure 1), but again the cause is not clear. In north east England effort also declined during the same period, butonce again it is not clear if this caused, or followed, the decline in landings. It is obvious that the accurate description and analysis of these events has been handicapped by inadequate fishery and biological data.

Monitoring and measuring abundance.

Given the above limitations and uncertainties, one short-term approach to safeguarding stocks is to monitor stock directly using selected fishermen in each district to record area-specific catch and effort on log sheets. The data should preferably be collected by fishermen whose

boats, gear, fishing practices, and fishing areas do not change over time. The underlying assumption is that pot catch per effort is a linear function of lobster abundance on the ground, and is not biased by density-dependent inter- or intra-specific behavioural interactions, or by a non-linear relationship between fishing effort and fishing mortality. A detailed investigation of these factors is in progress, e.g. Miller and Addison (1995); Fogarty and Addison (in press).

Management methods

UK lobster fisheries are managed by a minimum landing size (MLS), backed up in some local areas by a ban on the landing of berried females. The European Union allows the option of enforcing total length or carapace length, and the UK adopts the latter option, as being a fully rigid measurement. The UK national regulation is 85 mm carapace length, which for most areas other than South Wales (See Free, this volume) approximates to the mean size of first sexual maturity. Regional increases to 87 mm and even 90 mm are in progress in some areas. To improve future conformity with the MLS regulation by part-time fishermen, the adoption of escape gaps is being considered (Lovewell and Addison, 1989), but for pot fisheries which catch a mix of species, there are problems in finding a single size of gap which corresponds simultaneously to the MLS of lobster, edible crab, and velvet crab, three species with very different body size and shape.

The berried hen legislation, formerly adopted nationally but rescinded in 1961, was discredited by fishermen scrubbing the egg mass, and by scientific doubts about the likely benefit to recruitment if settlement and pre-recruit survival were affected by density dependent factors. It is recognised that this may not be a prudent approach in unregulated fisheries with high levels of effort, and a experiment to investigate the abundance of berried females using 'v' notching a tag-recapture tool is being planned for one area on the north-east coast following the adoption of this approach in Maine, USA (Daniel *et al.*, 1989), and the start of a similar project in Ireland.

The effect of adopting a maximum as well as a minimum landing size was modelled by Bannister and Addison (1986), but the maximum size approach has not been pursued in the UK.

In general UK lobstermen favour the introduction of a licensing scheme to limit entry to the lobster fishery, and discussions on the best method of achieving this objective are currently in progress with officials.

Stock enhancement

Many UK lobstermen favour the adoption of lobster stock enhancement as an approach to management, but it is not clear if they see this as a substitute for, rather than an addition to, more conventional management measures, nor wether they are prepared to contribute to the costs. The substantial biological results of the last ten years of enhancement experiments in the UK have now been made available e.g. Burton (1993); Bannister *et al.* (1994); Anon (1995) and Cook (1995), and are in the process of being evaluated by fishermen and by economists. However, preliminary plans for enhancement schemes in several local areas are yet to be fully developed, funded, and put into practice.

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Fishery and management of the lobster (*Homarus gammarus)* in Norway.

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Biology and climatic conditions

The European lobster *Homarus gammarus* reaches its northern limit in the coastal waters of Norway (Fig. 1). The summer temperature in the sea along most of the coast may be below 15° C, probably too low to support larval and juvenile development (McKenzie 1988) Cold water (below 15° C) during the summer is the rule in northern Norway, but can also occur in western Norway. Only along the southeast coast of Norway, is the sea temperature high enough to allow for annual recruitment. Even small climatic changes will probably have a major impact on successful natural recruitment.

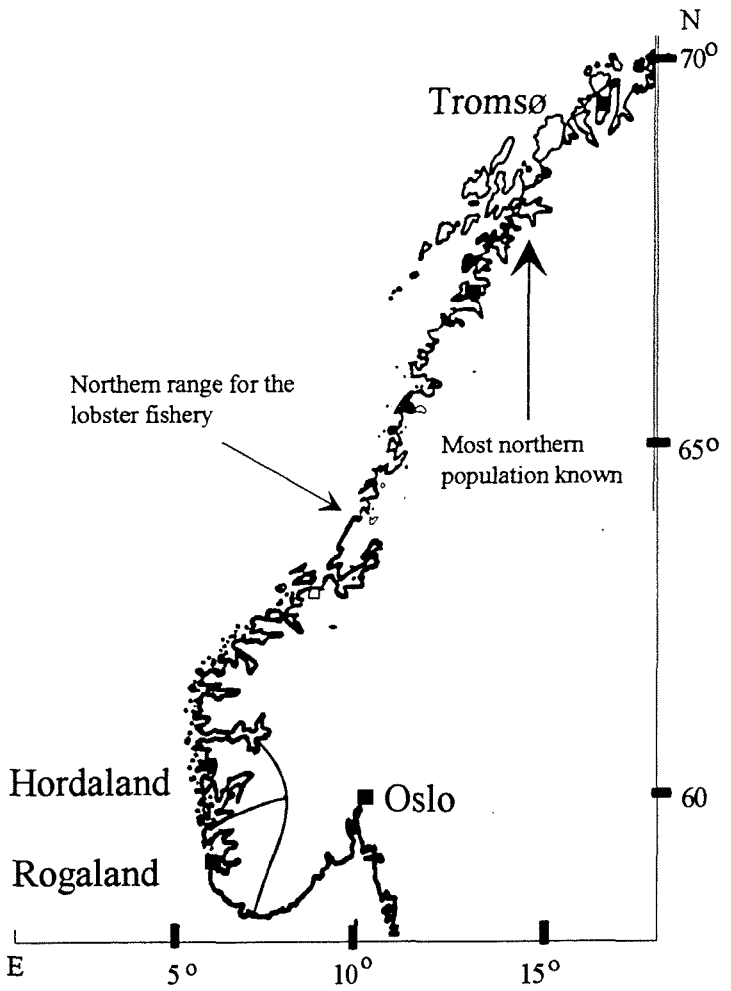

Figure 1. The lobster distribution in Norway.
Figur 1 Hummer utbredelsen i Norge

Lobster fishery

The fishery started between 1600 and 1700, as an export trade with the Netherlands until 1775 and England from 1776. (The historic events up to 1935 are based on Boeck 1869; Appelöf 1909; Dannevig 1936). After approximately 50 years of increasing landings, fluctuations commenced, first in south-western Norway, where the fishery had active for the longest period of time. A decreasing trend in landings was obvious in the late 1700s. The negative trend continued until the 1807-1814 Napoleonic Wars, which closed down the lobster market in England. It also made the coast unsafe for fishermen because of the British blockade of the coast of Norway, which was of the kingdom Denmark-Norway and in alliance with France. These seven years of protection made the lobster landings very good after the war, but within 15 years a new decrease started and continued until the lobster fishery during the summer was stopped by law in 1849.

After an increase in landings, with a mean annual landing of 1.5 mill lobsters in the 1860s, another decrease started in the 1870s and continued until the 1890s, when the trend reversed and the landings over the next 30 years stabilised and slowly increased, fluctuating between 500 000 and 1 million until the late 1920s (Appelöf, 1909; Dannevig, 1936). In the 1920s the increase was partly due to the lobster fishery starting up in new areas. In 1932 landings totalled 1 313 metric tons, which was a all-time-high record (fig. 2).

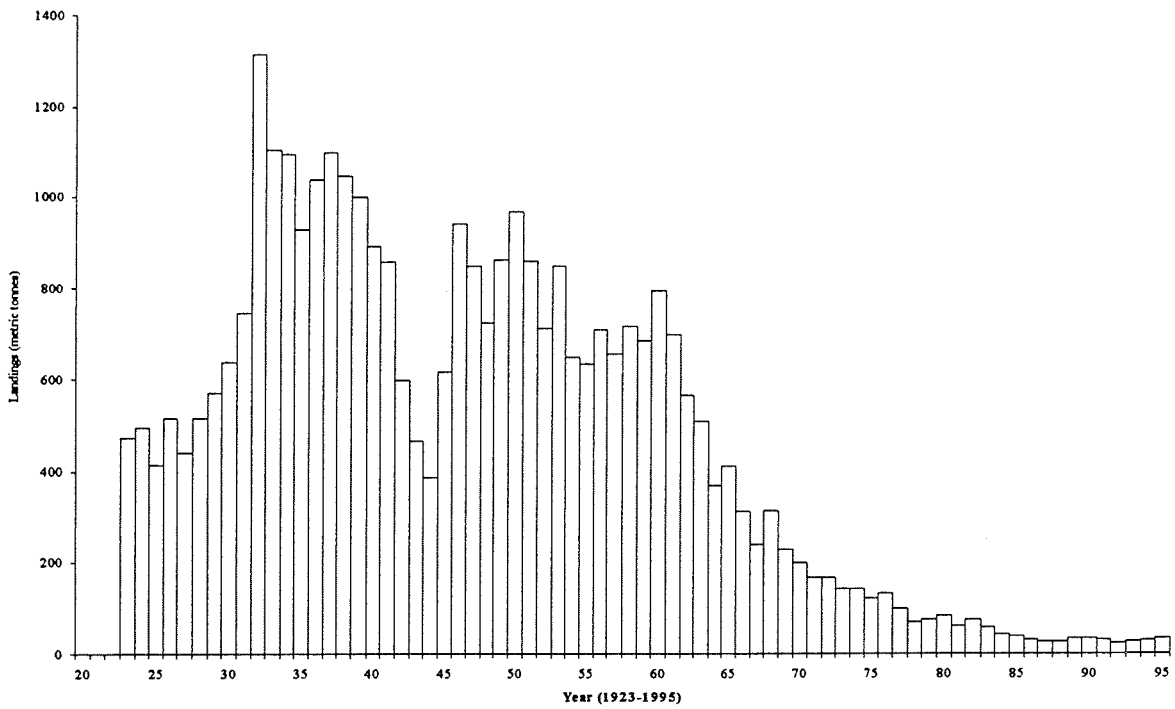

Figure 2 Lobster landings in Norway 1923-1995. (Source: Norwegian Directorate of Fisheries, Graphic presentation: H. Næss & A.-L. Agnalt, Institute of Marine Research)

Figur 2 Hummerfangster i Norge 1923 - 1995. (Fiskeridirektoratet Fig. H. Næss & A.L. Agnalt, Havforskningsinstituttet)

A study carried out on the south-eastern coast of Norway revealed that a mean of 44% of local stocks were fished every year (Dannevig, 1936). Since 1928, 30 to 50 fishermen along the Skagerak coast have filled in logbooks for analysis at the Flødevigen Marine Research Station.

Before the Second World War these books, as well as the landings, showed a decreasing trend in catch-per-trap-day (CPUE). After the peak in 1932, landings decreased to about 800 metric tons in 1940-41, when the fishery was severely reduced until 1945, due to wartime restrictions and a lack of necessary material for fishing (Fig. 2). After exceptionally good catches in 1945, annual landings decreased from 1000 to 600 metric tonnes in 1960. The fishery was still profitable. Landings then fell dramatically to 200 metric tons in 1970 and stabilising at 30 tons since the 1980s. Still unpublished data from the fishery at Kvitsøy between 1993 and 1995 indicates that more than 40 % of annual recruitment to the local stock is still being fished every year.

From 1948 onwards the length of unsorted lobster catches at five locations along the Norwegian Skagerak coast have been measured. Figure 3 shows a considerable change in catch composition. During the first 15 years (1954-63 and 1964-68) more than half the catch was below 240 mm TL, (85 mm CL). These size groups subsequently reduced their contribution gradually to the low level for the five-year period 1979-83, after which the percentage increased for the last 10-year period, 1984-93.

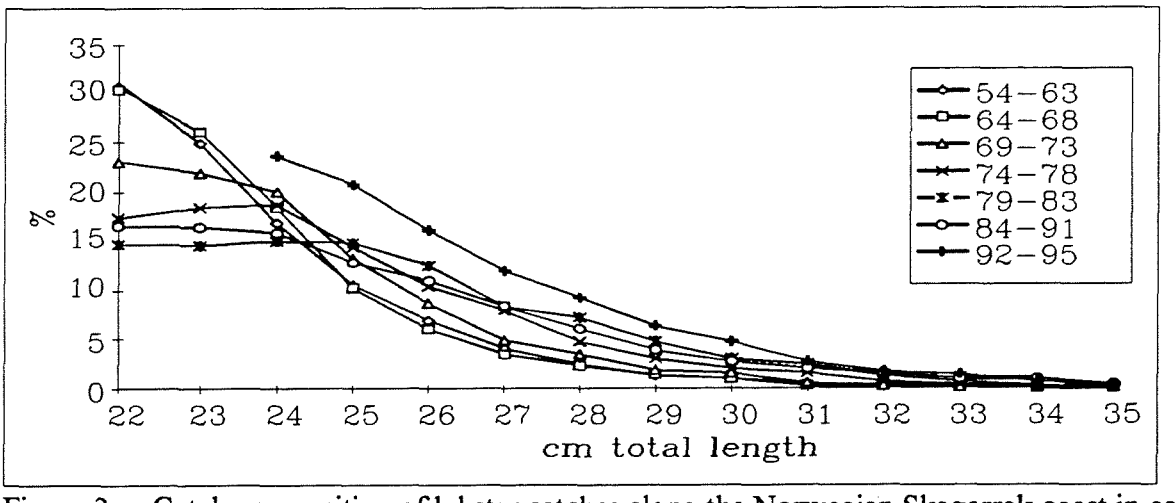

Figure 3. Catch composition of lobster catches along the Norwegian Skagerrak coast in each of seven periods; 1954-63; 1964-68; 1969-73; 1974-78; 1979-83; 1984-91; 1992-1995.

Figur 3 Størrelse fordeling av hummer fanget langs Sør-Øst Norge i hver av syv tidsperioder; 1954-63; 1964-68; 1969-73; 1974-78; 1979-83; 1984-91; 1992-1995.

Since this gradual change occurred simultaneously with the reduction in CPUE, the reason must be reduced recruitment. Tagging of lobsters from 200 to 240 mm has shown that natural mortality is very low (Rørvik and Tveite, 1982). Thus at least yield per recruit will increase for minimum sizes up to 250 mm (87 mm CL).

The reasons for the large fluctuations during the past 100 years are not clear. The regulations from 1879 (minimum legal size (MLS) 210 mm total TL) and 1893 (enforced closed season) might have had positive effects. The economic depression might be involved, giving unemployed people an opportunity to earn some money from the lobster fishery and causing an increase in fishing effort and landings. Traditionally the lobster fishery was limited to"good lobster grounds", and sections of the coast were left with low fishing effort. The recruitment might have been dependent on these natural sanctuaries with low fishing pressure.

In the 60s, people started to use the coast for vacations. Small privatly owned motorboats became popular. More than 400 000 small boats i.e. not registered as fishing boats are currrently in use along the Norwegian coast, almost one per 10 inhabitants (Central Bureau of Statistics of Norway, 1992). A large proportion of Norwegians spend their summer holidays and other vacations fishing along the coast. Lobsters are fished unregistered both in summer despite the regulations, and in the fishing season. Since the MLS was set below maturation size until 1992-93, increased fishing effort must have depleted the stock of mature lobsters, leaving few recruits to survive to maturity.

The landing statistics have always been unreliable (see C. Bannister in this volume), and are becoming even more so today. Spare-time fishermen land the bulk of the catch and even professional fishermen might sell their catch outside the legal channels, due to low holding capacity by the few remaining lobster dealers. The low landings for decades has forced many lobster dealers to close down, and the annual registrations since the 90s have probably reflected the maximum capacity of the few remaining lobster dealers more than the true landings. Still, the Norwegian lobster fishery can be regarded as a marginal fishery on a heavily overexploited stock. At the turn of the century, registered landings are only 3% of 1960 levels, while over the same time period the catch-per-trap-day in south-eastern Norway was reduced to 60% of the 1960 level.

Management

Regulations of the fishing season and MLS was suggested as far back as in 1737 by local authorities in important lobster fishing regions. However, no regulations were made by the Government until 1849, when the seasonal limits were adopted from 15 July until October. In 1879 the MLS of 210 mm total length (TL)(71 mm CL) was introduced. Despite several proposals for an increase in MLS, no change was made until 1964.

The MLS was increased from 210 mm to 220 mm TL (71 to 75 mm CL) in 1964 in the hope of stopping the reduction in CPUE. This was not successful since 220 mm is below the female maturity size. Only in the eastern part of Skagerrak are a few females below this size berried. During our period of registration the CPUE has been at a higher level in this area than in the rest of Norway. This shows that the MLS probably has an effect on recruitment.

Until 1992, the MLS was set below this size, causing exploitation of immature lobsters for nearly three hundred years. The reasons why the lobster stocks lasted until the 1950s, might have been due to large unfished areas outside the "good lobster grounds". A larger number of small but faster boats have been fishing along the coast during the past 40 years, leaving no parts of the south and western coasts unexploited.

In 1992 new regulations were passed, raising the MLS to 240 mm TL (85 mm CL) in south-eastern Norway and 250 mm TL (88 mm CL) in western Norway, which is above maturation size (Anon, 1993; Appelöf, 1909; Dannevig, 1936; Tveite, 1991).

More intense control efforts have reduced the illegal fishery, and effects of the 1992/93 legislation have already been recorded in terms of weight per trap in the Skagerrak area. In the future we can hope to observe increased recruitment.

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Fisheries and management

Discussions

The decline in Norway's commercial landings from more than 500 t early this century to just 30 t now is of concern to managers and may point to recruitment over-fishing. Sweden has seen similar declines except that in recent years it has experienced an improvement in catch per unit effort, possibly the result of management changes. Recent changes in minimum legal size in Norway may also have brought about an increase in mean size of lobster, a change viewed as being very positive.

Density dependent growth and survival, and the existence of 'bottlenecks' to survival at various life-history stages, need to be identified for Norway. Bottlenecks may differ from area to area. Water temperature may also be a particularly important factor for all life history stages of lobster in Norway. It was recognised that natural mortality rates may not be constant from year to year.

To assess lobster stocks in Norway two stock assessment models were suggested, although not mentioned in the review presentation - the Leslie method and Surplus Production modelling. Both have limited use because of the assumptions and data limitations.

This reflects a well known problem in invertebrate fisheries management. In fisheries based on traps, the trap catches do not measure actual abundance of animals on the sea floor, only actively foraging individuals. It is a need for fishery independent assessments of lobster abundance. Trap selectivity and performance studies are required, and there is the need for good series of catch and effort data and length frequency distribution data.

Genetic studies underway are useful in determining stock structure and in checking that genetic characteristics of with the wild stock is maintained where cultured larvae are released. Attempts should be made using genetic techniques to follow any larval migration between stocks.

Lobster stock enhancement investigations 1983-1993

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Summary
The feasibility of supplementing natural lobster stocks with hatchery reared juveniles was examined in Britain during the period 1983 to 1993 by the Ministry of Agriculture, Fisheries and Food (MAFF) at Bridlington Bay, on the English east coast. The video presented here (Wickins et al., 1995) was produced in order to provide easily understood, qualitative support for the more quantitative technical report describing the techniques developed by MAFF Directorate of Fisheries Research for rearing, tagging, transportation and release of the lobsters (Beard and Wickins, 1992). Additionally, it illustrated the quayside monitoring and tag-reading processes used in these and other British lobster stock enhancement trials (Anono, 1995).

Trials involved the mass production and release of juveniles, each tagged with an internal microwire tag, over the five years from 1983 to 1988. Juveniles were released onto areas of seabed previously identified as a suitable juvenile lobster habitat (Howard, 1988). Returns in commercial catches and from targeted fishing were monitored from five to ten years after release, i.e. from 1988 to 1993. At the same time work began on analysing the returns of tagged lobsters and conducting complementary experiments both in the laboratory and in the fishery.

The minimum numbers of lobsters needed to yield a useful number of returns was estimated to be 10,000 lobsters per year for five years (Beard and Wickins, 1992). At the hatchery, the size of the available rearing facilities dictated that each year the lobsters would have to be reared in two consecutive batches of 5,000 animals. This, combined with the desire to release the animals when sea temperatures were over 10 °C, dictated that production runs were timed to produce animals for release in May and September of each year. The smallest lobsters that could be tagged with consistent accuracy was 9-15 mm carapace length, thus, the stocking and husbandry regimes were scaled to meet this release size.

The rearing processes were conducted in five separate open recirculation systems; one broodstock system, two larval culture units and two on-growing systems. For two months prior to the introduction of animals, the biological filters in each recirculation system were "matured" by the daily addition of a solution of ammonium citrate in fresh water. This chemical encouraged the development of microbial growths that oxidised both organic and inorganic nitrogenous wastes. Wild-caught, egg-bearing females were purchased from merchants in February/March and again in September/October of each year. Females were only purchased from merchants known not to have a previous record of diseased stock. At the laboratory they were housed in equal numbers in two raceways in an open recirculation system supplied with a continuous flow of filtered, natural sea water for seven (February/March broodstock) to 18 weeks (September/October broodstock).

Upon hatching, the larvae were collected and stocked into two separate larvae culture systems each fed from a different water supply as a safeguard against failure. Each vessel was stocked sequentially with newly hatched stage 1 larvae at densities of 25 and 37 larvae l^{-1} (2000 and 1500 larvae per vessel for the 100 and 40 l vessels respectively). In order to reduce size differences and avoid cannibalism during the later stages of culture, each vessel was stocked with larvae hatched within a two-day period. After about two weeks the newly moulted stage 4 lobsters were easily distinguished from the pelagic larvae (stages 1-3) because they swam forwards with claws held out in front and with the dorsal side uppermost. They were removed individually to the on-growing systems the day they appeared. All larvae were fed twice daily with mysid shrimp *(Neomysis sp.)* purchased in frozen blocks from aquarist suppliers. Most larvae developed to the 4th stage within 11 to 17 days. Close attention to feeding and tank hygiene during the larvae culture phase proved to be critical.

As with larval stages, two independent on-growing systems were stocked to reduce the risks of failure. Each rearing trough contained four trays supported above the bottom of the trough on plastic 90° angle strips. Each tray contained 80 individual rearing compartments. Good water exchange to each lobster was ensured by a system of tidal flushing. The trays were stocked with stage 4 juveniles on the day they metamorphosed. As far as possible healthy animals with a full set of appendages were selected but occasionally it was necessary to include lobsters with claws missing to make up the numbers. They were fed mysids, shrimp and small pieces of *Mytilus* gonad tissue prepared from freshly shucked, live mussels (Wickins *et al.*, 1987). One feature of hatchery-reared lobsters was the lack of crusher claw differentiation in about 60% of some populations. It was felt that lobsters released with two cutter claws might not be able to utilise fully all food resources potentially available to them in the wild. The simple expedient of providing bivalve spat or an alternative hard food material rapidly stimulated crusher claw development in time for release (Wickins, 1986).

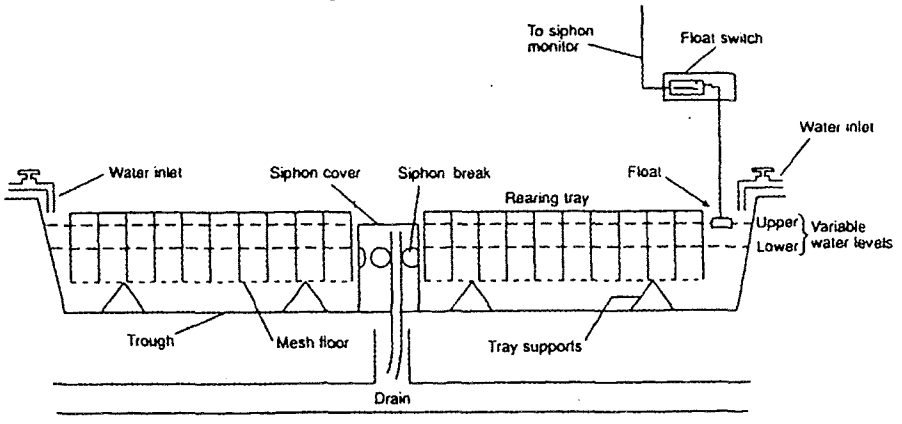

Figure 1 Longitudinal section through a juvenile rearing trough showing trays of 80 compartments, siphon and float switch arrangement. (Source: Beard and Wickins, 1992)

Figur 1 *Tverrsnitt av et yngeloppdrettskar som viser brett med 80 rom, overløp å flotørbryter. (Kilde: Beard and Wickins, 1992)*

The rearing programmes conducted at Conwy and elsewhere in Britain have shown that with meticulous husbandry and diet selection few problems are encountered during rearing of the juveniles from about stage 6 through tagging to transportation and release. Nevertheless,

erratic survival during incubation, larval rearing, and in the first one or two juvenile stages did occur and resulted in serious losses in all hatcheries at some time or another. Subsequent research indicated several prospects for optimising lobster production in hatcheries (Ali and Wickins, 1994; Wickins *et al.*, 1995). Specifically:

i) egg-bearing females should not be exposed to salinities below 30 psu;
ii) only early developing individuals at egg, larvae and juvenile stages should be selected for on-growing prior to restocking;
iii) supplements of good quality, live *Artemia* nauplii should be used in larvae cultures to replace prepared food supplements (e.g. chopped mussel) that pollute the water and increase the risks of infestation by epibiotic organisms.
iv) juvenile lobsters should be reared under feeding regimes that incorporate twice-weekly supplements of live or fresh foods.

After approximately three months, all lobsters were tagged internally with stainless-steel wire microtags using proprietary fish microtagging equipment adapted for use with juvenile lobsters by making a special head mould and by slightly altering the machine's injection cycle (Wickins *et al.*, 1986). The criteria for deciding the position of tag implantation were that the tag should:

i) cause minimum damage to the lobster;
ii) not be subject to loss by autotomy (spontaneous limb loss);
iii) be placed in a part of the lobster not normally eaten but large enough (in juveniles) to accept the hypodermic needle;
iv) be placed in such a plane that it passed through the tag detection apparatus with its long axis parallel to that of the detector rather than orthogonal to it.

Experiments had previously shown that tag retention was 85-100% as the animals grew through up to 22-29 moults (90-102 mm carapace length) in captivity. The studies also showed that tags could be placed accurately and retained in lobsters as small as 9 mm carapace length. Claw loss during handling was reduced from 4% to less than 1% at a tagging rate of 240 lobsters per hour as experience was gained.

After tagging and approximately seven to 14 days prior to release, the temperature of the rearing water was lowered by increasing the rate at which new, cold seawater was bled into the system. The rearing trays were stacked together and placed in covered tanks of circulating, aerated seawater for transportation by road to Bridlington Habour.

On arrival at the harbour, the tanks were off-loaded into a quayside net store to await transfer to the chartered vessel and subsequent release. During this period of four to 10 days the seawater was circulated by a submersible pump in each tank.

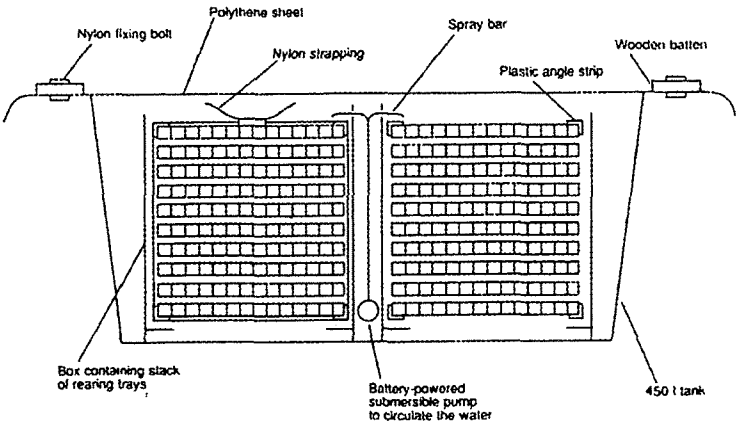

Figure 2 A transportable recirculation system capable of holding 1 280 individually confined three-mouth-old lobsters. The nylon strapping on the right-hand stack of trays has been omitted. (Source: Beard and Wickins, 1992)

Figur 2 Tverrsnitt av et yngeloppdrettskar som viser brett med 80 rom, overløp å flotørbryter. (Kilde: Beard and Wickins, 1992)

Areas suitable for release were located initially by side-scan sonar or echosounder but more accurate surveys were made by drift diving. The chosen areas were reefs formed of cobbles and boulders which provided plenty of crevices and thus initial protection for the juveniles while they began to burrow (Howard, 1988). The rate of release was intended to deliver a maximum of 2 lobsters per square metre, but lobsters were often seen to land at much higher densities. Some of the releases were made using a different method developed by the North Western and North Wales Sea Fisheries Committee during their parallel operation in Cardigan Bay (Cook, 1995). Essentially, the lobsters were sent one by one down a pipe trailing from the surface to the sea bed as the vessel drifted over the chosen release site.

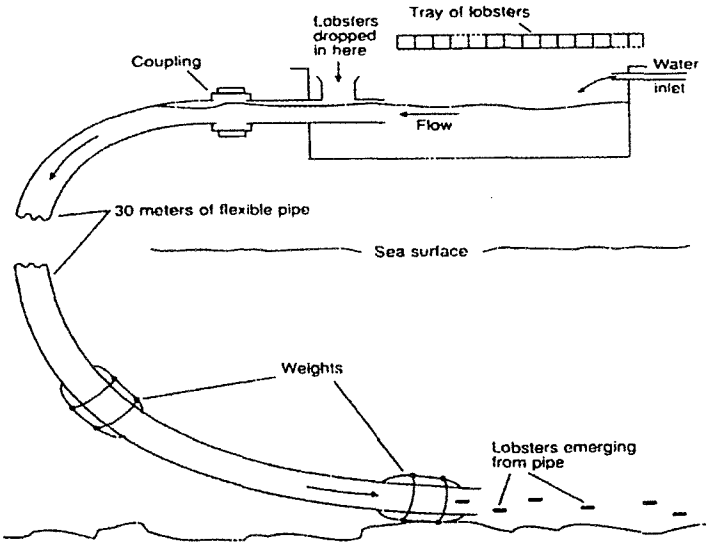

Figure 3 The arrangement used to release lobsters through a 30 m length of pipe. (Source: Beard and Wickins, 1992)

Figur 3 Oppsett for utsetting av hummer gjennom et 30 m langt rør. (Kilde: Beard and Wickins, 1992)

Catches were monitored at commercial landing sites, or were collected at sea by scientists on board boats fishing in release areas, for five years ending in 1993. Caught lobsters were passed through a sensitive metal detector and those giving a positive indication were taken to the laboratory and x-rayed to locate the tag which was then dissected out and read.

Most recaptured lobsters were clustered close to the original release positions and included several egg-bearing females. Preliminary calculations indicated that survival from release at three months of age to recapture at around five years could average 50% or more (Bannister *et al.*, 1994).

This study was the first to provide quantitative evidence that juveniles released into the wild could survive to minimum landing size in substantial numbers, be caught in baited traps set by commercial lobstermen, and contribute to commercial landing and to the wild breeding stock.

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Homarus
vethet

Lobster stock enhancement in Norway, with emphasis on a large-scale release project at Kvitsøy

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Introduction

Norway, situated at the northern limit of range of the European lobster, seems to have a vulnerable lobster population. The Norwegian lobster stock is depleted and has been so for more than twenty years. Release of intensively produced juveniles have been considered as a valuable method to enhance the stock and possibly develop a viable sea-ranching industry (Carlson 1954). Releases of untagged lobster juveniles and larvae have been carried out on several occasions for more than 100 years in Norway (Sund, 1915; Dannevig, 1928) and both private persons as well as industrial interests have been involved. The largest lobster hatchery in the world was build by commercial interests (Timar a/s) in 1981 (Grimsen *et al.*, 1987). The first one-year-old lobsters released in Norway by Timar a/s, should be recognised by having two scissors claws, instead of on scissors and one crusher claw. From 1983 to 1986, 200,000 juveniles were released all along the coast by Timar a/s. Unfortunately, only in two places, the lobster landings has been investigated after the releases, Mandal (Tveite 1992); Tveite & Grimsen, 1990) and Kvitsøy (van der Meeren & Næss, 1993) (Fig. 1)). Due to large natural variation in claw shapes, reliable counts has not been possible. Still, up to 50 % of the landings from the release area around Mandal were probably lobsters released in 1990 (Tveite, 1992).

Several lobster releases have been conducted in the UK (Addison & Bannister 1994; Bannister *et al.*, 1994) and some in France (Latrouite & Lorec, 1991). The Institute of Marine Research (IMR) in Norway took over the Timar Hatchery at Kyrksæterøra and started its research on lobster stock enhancement by releasing microtagged lobster juveniles. Due to the scale of the Norwegian lobster stock enhancement programme, and the environmental and geographical differences between the countries, caution is necessary when comparing the UK to the Norwegian results. The Norwegian programme aims to find wether releases of intensively produced lobsters can enhance a depleted stock, and if so, the results are essential for evaluating the potential of commercial lobster ranching. The project was financially supported by the Norwegian Sea Ranching programme- PUSH.

The first releases took place in 1990. The programme lasted until 1997, concentrating on recapture monitoring from 1994. This contribution provides general information about the project and the preliminary results on recaptures of tagged lobsters in the first part of the recapture period, including the 1995 lobster fisheries at Kvitsøy.

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Juvenile production

Lobster production in the large-scale release projects in Norway, as elsewhere, was based on wild females with external egg clutches. The lobster juveniles released by IMR came from a broodstock caught in the release areas. Juvenile production was conducted in the large-scale hatchery at Kyrksæterøra (Grimsen *et al.*, 1987) These juveniles were kept in separate boxes with flowing sea water until hatching. The larvae were removed from the hatching boxes immediately after hatching and transferred to 250 l bins with flow-through water. These bins produced large variations in survival rate, usually less than 5 %. Releases of stage IV and V juveniles (settling stages) directly into the sea have never resulted in significant increases in landings. Around 1980, a large-scale hatchery and holding equipment were build by Timar a/s to keep the juveniles up to one year old (Grimsen *et al.*, 1987). The settling larvea at stage V were transfered one by one to small, floating boxes for ongrowing until release six-11 months later. Survival was usually good, 60-70 % after seven months was common in the large-scale release project in 1990-94. (Uglem, 1995). Since 1990, shellsand has been provided in the juvenile boxes to encourage the development of crusher claws in the juveniles.

This was a costly production method, and other methods are discussed and are now used at the Shellfish Laboratory in Carna, Co. Galway, Ireland. This method keeps newly hatched larvae in 70 L hoppers with stagnant, vigorously aerated water, which prevents the larvae from attacking each other. Survival rates between 40-50% are reported (Mercer & Browne, 1994). Communal juvenile rearing would reduce the space and water demands needed for individually rearing of lobsters, but is not tried out in Norway.

Tagging

Microtagging with "Bergmann-Jefferts" tags was comparable to the UK method (Wickins *et al.*, 1986). Each release batch was given separate coded tags. In the experimental releases test and control batches also had different coded tags.

Transportation

The juveniles were transported in thermal transportation boxes, filled with wet newspapers and cooled by a top layer of deep-frozen papers (van der Meeren, 1991a). The transportation boxes were sent by air to the release areas. Transported juveniles were given 30 min to acclimatise in tanks filled with ambient sea water (van der Meeren, 1991b), before they were "sown" in shallow water (2-5 m) from small boats cruising along the shores.

Releases

Most releases were undertaken in March and April (Tab. I and II), omitting releases in summer and autumn, when predator density is high (van der Meeren *et al.*, unpubl. data).

The lobster juveniles were released along the shore in water less than 10 m deep, mainly in April, and some in March, June and December. The most wave-exposed coast lines were avoided by the fishermen, who released the lobsters by «sowing» them while cruising slowly along the shore in 18-20 foot open fishing boats.

In the large-scale release project two areas were chosen; Kvitsøy (large scale releases; (fig. 1)) and Øygarden (experimental releases). The releases at Kvitsøy were conducted as a co-operation between the Institute of Marine Research, Kvitsøy local authority and the local Fishermen's Organisation.

Experimental releases

The smaller-scale releases in Øygarden took place from 1991 to 1993. A total of 21 830 lobster juveniles were released in three year-classes and in the course of six releases. Transportation and acclimatisation processes were as for the large-scale releases. Some releases were conducted through a water-fed tube and some as "sowing" on to the surface. The aim of the experimental releases was to investigate how released lobster juveniles would survive immediately after release and establish themselves when released at different times of the year; in high and low densities; in wave-exposed versus sheltered areas; and several times a year in the same location. Monitoring was done by divers and target fishing by the Institute of Marine Research until 1995, both at the time of release, and periodically later on, but due to financial cuts, these experiments had to be abandoned to allow for the research activity needed to monitor the large-scale releases at Kvitsøy

Large scale releases

Six year-classes of lobster juveniles were released from 1990 to 1994, making a total of 125 588 juveniles in 11 separate releases. Kvitsøy was divided into six areas, to allow us to compare recaptures in the different locations (fig. 1). The releases were mainly done at locations 1-5.

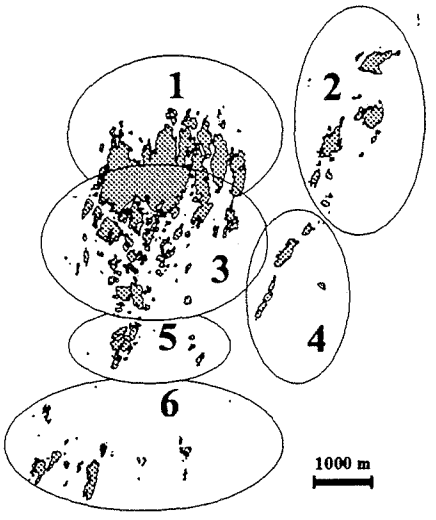

Figure 1. Map of Kvitsøy and the six subareas within the archipelago.
Figur 1. Kart over Kvitsøy med markering av seks gjenfangstområder.

Monitoring of recaptured lobsters

Monitoring of the large-scale releases started in 1991 and is continuing, in close co-operation with the local fishermen and the Kvitsøy local authority. A research team from the Institute of Marine Research and a local contact person from Kvitsøy local authority monitor all landings during the fishing season. The contact person is in close contact with both commercial fishermen and those fishing for leisure and private use. All lobsters landed are tested for microtags with a tubular magnetic detector from Northwest Marine Technology, making an audible sound when a microtag is passed through it. Tagged lobsters are bought by the Institute of Marine Research for further analysis and tag retention. A reward is also paid for tagged, legal sized lobsters (approx. NOK 25/ £ 2,5), lobster pins or caps.

All lobsters landed were measured and sexed. Measurements included: Carapace length (CL), Carapace width (CW); Total length (TL); Telson width (TW). In some cases estimates of Weight; Egg counts; Claw length, width and thickness in both claws were also made. The second pereiopod from the tail from all tagged lobsters and a number of wild lobsters was taken for genetic analyses.

A genetic analysis was also made of samples from the wild population, some of the broodstock used and the released juveniles. The genetic data are important for evaluation of any unusual genetic effects on the wild lobster population in question. Undersized lobsters were measured, given an individual external mark or tag and released in the same area as captured..

In 1991-1995 nearly all lobster catches in the Kvitsøy landings were run through the tag detector and the lobsters registered as described above, and some fishermen started to keep logbooks in agreement with the IMR. Monitoring of all lobsters landed on the islands and sub-sampling in localities around Kvitsøy started in 1994, and this will be followed up as a control to the Kvitsøy monitoring.

Preliminary results including 1995 fishery

The fishing season is split into two periods from March/April to 1 June and 1 October to December. In the spring season, relatively fewer undersized or newly recruited lobsters were caught, compared to the autumn fishery.

The recapture percentage in the spring fishery is therefore lower than in the autumn fishery. A substantial impact of the first release groups came in the autumn fishery 1994, with 26 % of the landed lobsters being found with microtags or having two scissor claws (fig. 2). The fraction of cultured lobsters in the landings have since increased year by year and reached 29 % in 1995. In the undersized lobsters the fraction of cultured lobsters rose to 65 % in 1995. However, landings of wild lobsters at Kvitsøy seems to be fairly stable.

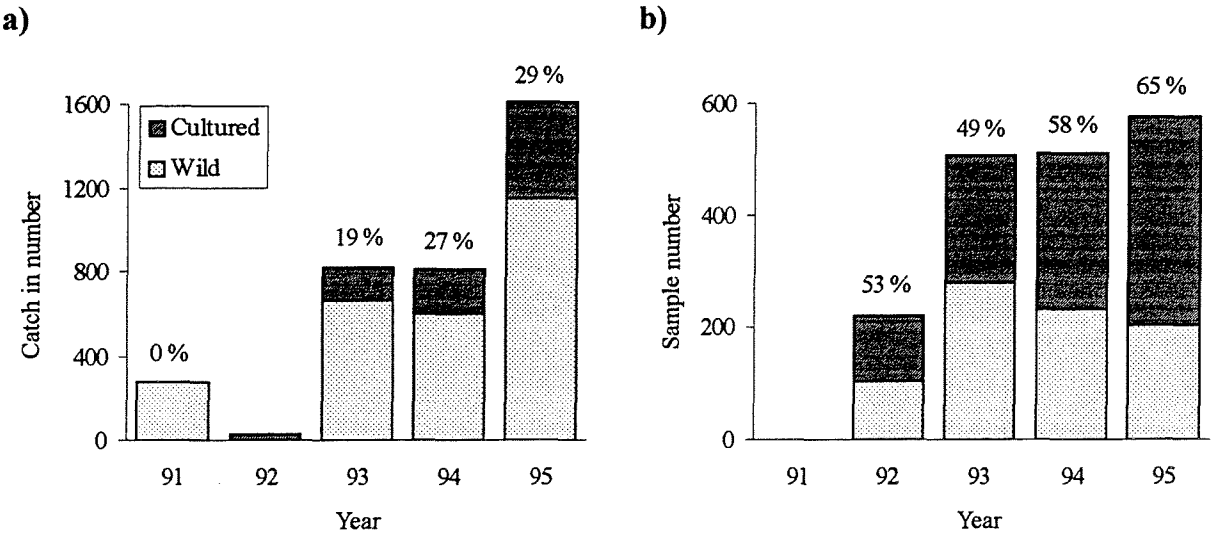

Figure 2. a) Lobster landings in the autumn fishery, and b) Subsamples of undersized lobsters captured, tagged and released by 1995. The upper bar is the cultured lobsters.

Figur 2 a) Hummerfangster i høstfiske, b) Prøvefiske av hummer under minstemål for merking og gjennutsetting høsten 1995. Øvre del av søylen viser innslag av utsatt hummer.

The cumulative recapture rate for the lobsters released at an age of 7,5 months in 1990 was about three percent in 1995, but is likely to increase substantially in the later recapture period. No recaptures of any released groups were registered before three years after the release. Only the first release groups have so far been detected in the fishery. Neither have any tagged lobsters been found so far outside the Kvitsøy archipelago. Cultured females captured with external eggs have been registered every year since 1993, some down to 71 mm CL in size but mostly more than 85 mm CL in size. Fishing effort in the Kvitsøy area has increased from about 1000 trap hauls per fisherman in in 1992 to more than 2000 trap hauls per fisherman in 1996, based on the logbooks kept by five selected fishermen.

Discussion

Final results of lobster releases in Norway can not be reported yet. In the Mandal release and earlier Kvitsøy releases by the Timar as, the fraction of probably released lobsters (having two scissor claws) have been up to 50% of landings four to five years after release (Tveite & Grimsen, 1990).

The large-scale releases at Kvitsøy have been by the traditional low-cost and quick surface-release method ("sowing") in March/April, with suitable weather and 30 min of acclimatisation to ambient sea water, in order to minimise loss to predators and intra-specific fighting. A summer release in 1988 resulted in greater than 10 % mortality within the first hour due to the high density of seasonally occurring predatory fishes (van der Meeren & Næss, 1991), and to the passive and infunctional behaviour of the lobsters as they emerged directly from the transportation boxes (van der Meeren, 1991a; 1991b).

The local population is now clearly influenced by cultured lobsters, as the cultured lobsters make up about 30% of the total landings. A careful comparison with other areas will continue

to be made in order to test if the Kvitsøy lobster stock has been enhanced rather than simply displaced by cultured lobsters at the expense of the natural lobster production in the area.

The economic aspect of lobster releases in Norway based on the techniques used in this large scale release is not favourable. The cost of producing lobster juveniles has been high. The recapture rate must therefore also be high, about 20-25% (Moksness *et al.*, in press) for the releases to be economically viable. Cheaper juvenile production, better knowledge of the habitat requirements of the juvenile lobster, and avoiding release of lobsters at higher densities than the carrying capacity of the location, are important problems remain to be solved, as well as the aspect of legal ownership of the released animals.

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Lobster stock enhancement

Discussions

Mass rearing of juvenile lobster of any size is now possible, but techniques need to be improved in order to decrease rearing costs and to allow enhancement to become economic. Particular problems are associated with the up scaling of production since larval mortality in the tanks used in Norway for large scale production are still too high. Better control of temperature and improved food should help.

Fitness of laboratory-reared juveniles for life in the wild is a major issue in enhancement programmes. Use of special (shell sand, oyster spat) substrates in the rearing boxes has led to reared lobsters developing crusher claws, as they do in the wild. Acclimation before release to the conditions which will be experienced in the wild, and low as possible stress levels, help in the successful transition of the juveniles to life at sea; these issues need to be further investigated. Communal rearing of stage IV and V lobsters may also lead to animals better acclimated for survival after release.

Both in UK and Norway, recaptures in the fishery of lobsters once released as juveniles (released nine months of age in Norway and three months in the UK) show that reared lobsters do survive in the nature. Egg bearing tagged females are also recovered, showing that reared lobsters can contribute to spawning. Since the meeting, an increasingly amount of data is coming in from the Norwegian release programme, which is reflected in the Norwegian paper in this chapter and in the final remarks.

More work is required to select the best habitat into which to release lobsters and the best stocking densities. Densities of newly settled lobsters in the nature vary geographically. In New England (USA) density may be as high as 5 lobsters per m^2 but similar estimates are not available for Europe. In Norway, lobsters have been released at 1 lobster per m of shoreline. Follow up of the Norwegian experiment gives important information useful in future releases acoording to time and place. Also information on release frequency and lobster density in a restricted area will be important in future releases.

No lobster stocking programmes was at the time of the meeting economically successful. More information is needed about the most economic size to release juveniles into the wild. Encouraging results have been obtained both in the UK and Norway. Survival and tag return rates may vary from area to area, so more returns are necessary before the overall economic feasibility of the programme can be judged.

Final summary

Recommendations

The aim for the meeting was to improve the understanding of the life history and ecology of the European lobster by presenting information on this wide range of topics, and to make recommendations to further research on the factors effecting the life history and ecology of the European lobster and hence the lobster fisheries.

The reviews and the Norwegian presentations on on-going research made together a base-line from which some of the most critical gaps in our knowledge were addressed. The input from researchers bringing with them expert knowledge from a wide range of lobster related topics made the discussions intriguing. In some topics the discussions were long, with some controversy, but most often the main concern for all participants was the lack of documentation on important aspects regarding lobsters biology, fishery management and restocking.

Several suggestions were made for the development of more effective long-term management strategies, based on carefully identified and well designed research projects.

Reconciliation of laboratory experiences is needed, particularly for larvae and juveniles. Raising larvae and juveniles of European lobsters in the laboratory has been done for decades in several countries, but much of the knowledge is not published and the contact between the hatcheries could be better developed.

Experiences from laboratory rearing can also contribute to increased understanding of what is important for larvae and juvenile survival in the nature. It is of great significance to unravel the 'bottlenecks' to survival of the various life history stages. The lack in ecological data on the life of the early benthic phase lobster in Europe cause concern, both for fishery managers and when releasing juveniles to enhance stocks. Density-dependent survival might be one of the crucial factors determining success or failure in a release programme.

In adult lobsters more need to be known about where and why lobsters stay or move in and between habitats. The relationship between the sexes is another topic which will be important to unravel, in order to assess the effect of fishery regulations concerning protection of females. It is of little use to protect females if their larvae production will be low due to lack of males that efficiently can fertilise their eggs.

Both aquaculture and fishery should benefit from better modelling of the variability seen in and between lobster populations. Evidence exist showing substantial geographical variation in size at onset of breeding, but many places, as in Norway, very little is known on this topic. Some studies of egg viability has been done in the laboratory, but not in a scale that give information that can be applied to analyses of natural reproductivity. Growth and survival at the various life history stages is still little known, but techniques as cuticle implantation and measure of accumulated fluorescent brain pigment are now developed, and will allow for improved possibilities for future investigations. It is important that investment is made in the development of sensitive and standardised analyses, making data obtained in one research programme comparable to results from other research programmes on the same topic.

Epilogue

Lobster research in Norway

In Norway the lobster population seems to have been through a more serious decline than the lobster populations around UK, Ireland and France. The Norwegian landings are now only 1/10 of what they were in the 1930's. Due to lack of knowledge of lobster biology, we do not know why or how the fishery overcame the natural recruitment, or why the stocks have not recovered years after large commercial fishery disappeared.

If we can understand what went wrong with the Norwegian lobsters stocks, we might in the future make the right decisions to prepare for the re-establishment of the stocks. Not only the Norwegian stocks would benefit from this. Better understanding of the natural history of the lobster, based on sound biological knowledge, would benefit lobster management throughout Europe.

It has been an increase in research activity in Norway the last 30 years, in particular since 1988 when research was initiated by the Institute of Marine Research on the release of cultured juveniles to enhance depleted lobster stock. This research has developed and today it covers almost all topics discussed at the meeting. After the meeting the international contacts also resulted in the initiative to several international research projects.

Fishery related studies

Lobsters have been fished in Norway for 350 years, but the management is still based on weak and scattered data. Except in the protected season, the lobster fishery is open for everyone as long as they adhere to the minimum legal size. In Ch. 5 the fishery and management history is briefly presented, as well as some indications over how the latest regulations, bringing the minimum legal size up to 88 mm CL and above the size of maturation in the females, from earlier 83 mm CL, can have positive effect on the lobster stocks.

Monitoring of selected lobster locations all along the Norwegian coast, as well as fishery diaries kept by selected fishermen have been undertaken over several years, in some cases since the 60's. The fishery is still difficult to assess, since not all landings are registered.

Hatchery and rearing

The hatchery was overtaken by the Institute of Marine Research in 1989 and the basic rearing procedure is described in Ch. 6 in this report. Along with the rearing of the juveniles to release, several experiments were undertaken in the hatchery.

Different sandy substrates was tested in the juvenile compartment, to see if any was more suitable than other to help the lobster in developing both crusher and scissor claws. These results was presented as a Master of Thesis at the University in Bergen (Korsøen, 1994).

Both the microtagging and the elastomer tagging techniques were experimentally tested (Uglem & Grimsen, 1995; Uglem *et al.*, 1996a). Medical treatment of the lobster eggs to obtain high survival rate of the larvea was tested (Uglem *et al.*, 1996b) and the occurrence of the polychaete *Histriobdella homari* found in the lobster egg batch (Lerch & Uglem, 1996).

Alternative rearing techniques were also developed at Flødevigen Research Station. Since 1997 a small-scale lobster hatchery has been running on Kvitsøy, small 70 l hopper with up-welling water current during the larval stages and growing the juveniles from stage V to X in small containers on the sea bottom. (Knudsen & Tveite, unpubl. data).

Enhancement

The large scale enhancement project from 1990 to 1997 is presented in Ch. 6 in this report and in several papers (van der Meeren, 1993; van der Meeren & Næss, 1991) In addition several papers are in press, discussing the fitness of reared juveniles to survive in the nature, and the economic potential of stock enhancement (Agnalt *et al.*, in press; van der Meeren, 1990; 1991; Svåsand *et al.*, in press; Moksness *et al.*, in press; Borthen *et al.*, in press). Work is being done concerning predation risk, morphological measurements, age at maturation, and fecundity. Monitoring of the local lobster landings for tagged lobsters will be continued at least though 1998 and hopefully for yet some years.

Genetics

At the commencement of the stock-enhancement program described by van der Meeren and Uglem (this publication) no genetic studies of European lobster, neither in wild populations nor in connection with releases of cultivated animals had been reported. It was therefore a clear need to perform such studies. In general, the investigated gene systems showed little degree of genetic variation. However, small but statistical significant changes have been observed in the allele frequencies when comparing wild lobster, brood stock and produced offspring. This study is still in progress.

Jørstad and Farestveit (in press) evaluated the genetic variation in 22 different populations along the Norwegian coast, and found minor but statistically significant variation in allele frequencies. The northernmost distributed population, in Tysfjord, contributed substantially to the overall sample heterogeneity. Further, recommendations for future commercial ranching operations of lobster were made.

A project initiated in 1998 aims to evaluate and assess the genetic influence of previously imported lobster from Scotland on local populations along the south-western coast of Norway. In addition, an EU project is to be implemented by the end of 1998, and intends to determine genetic diversity in European lobster regarding population structure and impacts of stock enhancement.

Age determination

A Norwegian project aimed at aging of lobsters by quantification of lipofuscin in the olfactory lobe was run by the Institute of Marine Research in 1995-96. The project was financed by the Norwegian Research Council and the activity is primarily aimed at examining if lipofuscin is a reliable age indicator also in European lobsters from Norwegian water. This was done by measuring the amount of lipofuscin in brains of lobsters with known age. These animals were originally reared and thereafter released and recaptured at the island Kvitsøy as a part of the

Norwegian Sea-ranching programme (see Ch. 6). The brains was analyzed both fresh and as wax sections with a laser scanning confocal microscope (Belchier *et al.*, 1994). Preliminary results show that it is a significant, but variable, increase in amount of lipofuscin in the olfactory lobe with increasing age also in lobsters from Norwegian water (Uglem unpubl. data).

As a result of the meeting at Kvitsøy in 1995, I. Uglem and Dr. P. Shelton ran a cooperative field work in 1996 injecting cuticle implantation into close to 100 lobsters at Kvitsøy. These lobsters were tagged with streamer tags and will be followed in the future monitoring of the fishery.

Juvenile ecology

All releases of lobster juveniles have been based on knowledge of juvenile ecology partly from laboratory observations and partly from data on the American lobster *Homarus americanus* . It is major differences between European coastal ecology and American, especially in the high biodiverstity in Europe compared to the north east cost of America (Wahle 1995). Also in the laboratory, lobsters have been sheltered from the other species normally encountered in nature.

Since the large-scale release at Kvitsøy, several diving surveys have been arranged to describe the variation in bottom types, and the biodiversity around these islands. This information will be related to the recapture of tagged lobsters from the release sites and if possible, also to compare growth and recapture rates between the sites.

As a result of the 1995 Kvitsøy seminar, and previous attempts to find juvenile lobsters in Ireland and the English Channel, an EU FAIR-sponsored research programme over three year was proposed by IMR Norway, CEFAS (former MAFF) in Lowestoft (UK) and the Shellfish Laboratory in Carna, County Galway (Ireland). The research programme «The influence of competitive interactions on the abundance of early benthic stage European lobster (*H. gammarus* (L.)) and hence on the carrying capacity of lobster habitat.» was accepted in 1986 when Italy was included and will go on from 1997 to 1999. The programme is aimed to investigate the ecology of the includes partners from northern, central and southern parts of Europe.

The work programme will

- Determine the patterns of abundance of juvenile lobster, competing decapods and potential competitors and predators (task 1)
- Investigate predation, and competition for food, by determining the diet of lobsters and its potential competitors and predators (task 2)
- Investigate predation on lobster in the field using a tethering experiment (task 3)
- Investigate competitive exclusion in the field between lobsters, and between lobsters and other decapods, by comparing survival at different lobster densities and in the presence or absence of other decapods (task 4)
- Investigate competitive exclusions in the laboratory by showing if lobsters and or potential competitors displace lobster from preferred habitat (task 5)

- Test if the density of lobster and of other decapods affects lobster survival and growth in the laboratory (task 6)

Behavioural ecology

The first release at Kvitsøy was with lobsters mainly with two scissor claws. Measurements of the claws in recaptured lobsters also showed that even the scissor clawed lobsters developed some dimorphy between their claws (van der Meeren & Uksnøy, in prep.). The lobsters with two scissor claws would with size have one claw significantly longer than the other claw and the scissor claw in wild lobsters of the same size.

In 1995 some of these were recaptured and their ability to compete with equal sized wild lobsters was tested. They lost significantly more duels than the wild lobsters, but this might be due to the smaller total claw index found in these lobsters compared to wild lobsters with both a crusher and a scissor claw (Uksnøy, 1995). Wild lobsters with lower claw index than their cultured opponent also tended to lose their fights.

As part of the running reseach at Kvitsøy, several hundred lobsters close to the minimum legal size are captured, tagged and released every year. Some unvoluntarely get released other places than where they were captured. A short-time tracking of four acoustic tagged lobsters indicated that lobsters are able to get back to their "home position" if the distance is from relsease spot to home position is within reasonable distance (as appr. 500 m in this test). If they were moved more than 2000 m, they established themselves close to the release spot (van der Meeren, 1997).

Tagging

Tagging is an important issue in field studies. The following is a summary of the different techniques tried within the large-scale release project at Kvitsøy, and the experiences made during the project.

The need for a small and safe tag, suitable to insert into very small animals to be released, was met by the adaptation of the North West Marine Technology inc. (NWM) coded microtags («Bergman Jefferts tags»), as presented by Ennis (1972) and Wickins *et al.* (1986) (fig 1). This is 1 mm x 0,25 mm (full length) or 0.5 mm x 0,25 mm ($^1/_2$ length), stain-less steel, magnetised tags. This technique has been used with success in several release studies, where the lobsters are tagged from stage V (newly settled) up to more than twenty months old, in hatcheries and ongrowing facilities, both in UK, Norway and Ireland (Beard & Wickins, 1992; Burton, 1992; Linnane, 1994; van der Meeren, 1994; Cook, 1995; Uglem & Grimsen, 1995).

The advantages of coded wire tags is that the tag is small, long-term tag retention is. Mortality is low, 1-4% (Burton, 1992; Uglem & Grimsen, 1995). The coding allows for comparisons between the different released groups (Addison & Bannister, 1994; van der Meeren, 1994). It is also possible to detect newly eaten lobster juveniles in the intestine of predators, by sending the fish through the monitor (van der Meeren, 1995). Increased predation of newly released lobster juveniles in the summer months, compared to the winter months has been detected using this method (Borthen *et al.*, in press).

The weakness of the tagging technique used in the lobster release projects, is that it can be used to code for group identification, not individuals. It is also an expensive technique, with the need of advanced electronic devices. Since the tags are not visible, recapture registration

must be based on a very good relationship with the fishermen, to be sure that they deliver all their landings for tag monitoring.

In behavioural studies, population estimates, migration studies, growth comparisons between wild and released lobster and growth differences between certain areas and sexes, external and individual tags are needed.

Since 1992 sub samples of the lobsters below minimum legal size are measured, given an individual external mark or tag and released in the same area as captured. Until 1994, small spots were branded in to the telson according to a numerical code (Abrahamsson, 1965) Branding was done by holding a soldering bold firmly against the exoskeleton for ten to twenty seconds, but not long enough to burn any hole in the carapace. This imply a reddish colour at the branded spot. After one moult, the spot turn white, and gets more bluish after the three to four following moults, when the natural colour returns. In addition to colour changes, the structure of the exoskeleton will be changed permanently (K. Gundersen, pers.comm.). This technique has been as a part of both a pilot release study prior to the large scale sea ranching project (van der Meeren & Næss, 1991; van der Meeren, 1994). Branded animals has been detected easily by trained personnel after more than three years in the sea. The advantage of this technique, is that it is non-invasive, leaving the lobster with marks without penetrating the exosceleton nor any membranes. The drawback is that the marbled pattern of the lobster makes the aged spot difficult to recognise, and it was never found by the fishermen. The method was abandoned after two years.

Floy FTL-69 Lobster tags (sphyrion tags) were tested one year. This is small tubular plastic tags, attached with a "T"- shaped anchor injected with a hypodermic needle through the membrane between carapace and telson, into the muscles inside. In a Norwegian small scale test the loss over the first moult was close to 20 % (unpubl. data). Approximately the same tag-loss has been described in other experiments (Cooper, 1970; Bennett & Lovewell, 1983; Ennis, 1986; Moriyasu *et al.*, 1995). It was also observed by us that some of the tagged lobster developed infections at the tagging spot. Thus, Floy tags were abandoned before it was used in the field.

Since 1994 the NWT elastomer tags has been used. Small droplets of the floating elastomer tag were injected under the dorsal membrane of telson by a hypodermic needle, in defined areas of each telson joint according to a code system. In 1995 an extra droplet was placed in the last joint of telson, for quick and easy determination of the individual as a tagged lobster. A new colour was used each year. While blue and green tags appear regularly in the catches, also years after tagging, the red tags are hardly seen. This might be due to a blending of the red tag by the naturally occurring red pigment commonly found in the membrane of lobsters in Norway. The tags can be easily detected by a UV-lamp, but the use of such lamps in the field are difficult. Another drawback with this tagging techniques, especially with the first generation tagging kit we had, was the time used to tag large number of lobsters with several tags each. A final and the most serious problem, is that the full code hardly was readable in recaptured lobsters. Elastomer tags have later been recovered from different parts of the lobster body, for instance from the gills. This tagging technique was abandoned after 1995.

Since 1996 streamer tags has been used. It is shown that streamer tags results in less tag loss than sphyrion tags in large lobsters *H. americanus* (Moriyasu *et al.*, 1995), Norway lobster *Nephrops norvegicus* (Chapman, 1982), and shrimps *Penaeus semisulcatus*, in Kuwait (Farmer, 1981). Due to the long term recapture period expected in the beginning of the large scale release project, we chosen not to use this technique in the early stage of the project, to

avoid marking small lobsters with tags that could be overgrown before we could recover them. Still, the technique was implied in 1995 by the use of Hallmark inc. streamer. In a small scale laboratory test, only one lobster died from bleeding, having got the tag placed wrongly. We regularly recover lobsters with streamer tags from the catches of the fishermen. They also register some, but not all, when the lobsters are removed from the creels. As for the other external tags, the streamer tagged lobsters are intended to be used in population estimates, migration studies, growth comparisons between wild and released lobster and growth differences between certain areas and sexes. Being the tag that is easiest to apply correct, recover and read, we expect the streamer tag to give more information the next years, than the other external tagging techniques. Fishermen also find this tag more often than any other external tag used.

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