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# Further evidence on biennial spawning of the Norway lobster, Nephrops norvegicus, in the Central North Sea

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## Abstract

The reproductive cycle of the Norway lobster, *Nephrops norvegicus*, in the Central North Sea was investigated from data on the relative frequencies of berried and hatching females, the landings per unit effort of male and female *Nephrops*, their sex-ratios, and the development of the abdominal eggs.

The results of the present study largely confirm the findings of earlier investigations in this field (REDANT, 1987).

Spawning takes place in September-November ; hatching in late spring and summer. The course of the reproductive cycle was found to be roughly similar in all size-classes of females. The percentages of berried females at the height of the spawning season however, were inversely related to the size of the females.

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This observation, together with the fact that the mid-winter catches always contained relatively large numbers of non-berried females, supports the hypothesis that the chances of skipping a reproduction cycle, and of shifting from annual to biennial spawning, increase with increasing size of the females.

Additional evidence to this hypothesis was found from the data on the development of the abdominal eggs.

Résumé

Le cycle de reproduction de la langoustine, Nephrops norvegicus, dans la Mer du Nord centrale a été étudié à partir de données sur les abondances relatives des femelles grainées et des femelles dont les larves viennent d'éclore, les débarquements par unité d'effort des mâles et des femelles, leurs sex-ratios, et le développement des oeufs abdominaux.

Les résultats de ces investigations confirment en grande partie les conclusions d'une étude antérieure et similaire dans ce domaine (REDANT, 1987).

La ponte a lieu en septembre-novembre ; l'éclosion des larves vers la fin du printemps et en été. Le déroulement du cycle de reproduction était semblable parmi toutes les classes de taille des femelles, mais les pourcentages maximales de femelles ovigères, en pleine période de ponte, étaient inverses à leurs tailles.

Cette observation, et le fait que les captures réalisées en plein hiver contenaient toujours un nombre relativement élevé de femelles non-grainées, supportent l'hypothèse que l'éventualité de sauter un cycle de reproduction, et de passer d'un régime de ponte annuel à un régime biennal, augmente avec la taille des femelles.

Pareillement, les résultats sur le développement des oeufs abdominaux ont permis de mettre en évidence cette hypothèse.

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## 1. Introduction

Biennial spawning has been reported to occur more or less regularly in the Norway lobster (Nephrops norvegicus) stocks around Iceland (EIRIKSSON, 1970) and the Faeroer (ANDERSEN, 1962), in the Farne Deep (SYMONDS, 1972) and more recently in the Clyde, west Scotland (BAILEY, 1984).

Around Iceland, where low ambient temperatures result in a prolonged incubation period of 12-13 months, biennial spawning is obviously the rule, whereas in the Clyde, under more temperate climatic conditions resulting in much shorter incubation periods, the onset of biennial spawning seems to be related to the size of the females. As the females grow their increasing size appears to retard recovery from moulting and ovary maturation, and - as an immediate consequence - their availability for mating. Eventually they may skip a spawning period and shift from annual to biennial spawning (BAILEY, 1984).

The occurrence of a similar spawning regime was suggested in an earlier paper by the second author on the reproductive cycle of Central North Sea Nephrops (REDANT, 1987). In order to verify these preliminary findings the investigations discussed in that paper were continued for another period of two years, and complemented with a detailed study on the seasonal development of the abdominal eggs.

## 2. Material and methods

### 2.1. Market sampling programme

Data on the relative abundance of berried and hatching (i.e. with remains of recently hatched eggs under the abdomen) females, the landings per unit effort (LPUEs) of male and female Nephrops, and their sex-ratios were obtained from market samples. These were collected at approximately forthnightly intervals, mostly in the auction of Zeebruges, the main home-port for Belgian Nephrops trawlers fishing in the Central North Sea (Botney Gut-Silver Pit area).

Details on the area of investigations and on the methods used to collect and to process the data can be found in REDANT (1987).

As with the previous investigations and for exactly the same reasons with regard to the discarding and marketing practices of the Belgian Nephrops trawlers, the analysis of the present data was also restricted to Nephrops > 30 mm carapace length (CL).

2.2. Abdominal eggs

Samples of the abdominal eggs were collected from all berried females in the market samples. The eggs were stored in small plastic jars and preserved with 5 % formalin, buffered with natural sea-water.

Preliminary experiments were carried out to determine the effect of formalin preservation on the volume of the abdominal eggs. For this purpose 15 samples of 50 eggs each were kept in formalin for a period of 24 weeks. Every two weeks, up to three months, and every four weeks thereafter the volumes of these eggs were computed from binocular measurements of their smallest (d) and largest (D) diameter, using the formula :

$$\frac{\pi}{4} \cdot d^2 \cdot \left(D - \frac{d}{3}\right) \qquad \text{(BRATBAK, 1985)}$$

The means for each sample were then compared to the initial mean volumes, measured prior to preservation, to give an estimate of the average change in volume.

The overall trend (i.e. the mean of the means) is given in Figure 1, together with the minimum and maximum figures for each set of data in the time series. The curves were smoothed by the build-in graphical features of the software used to plot the data (Harvard Presentation Graphics, version A.01).

Shortly after preservation the volume of the eggs increased by on average 5 %, with a minimum of almost minus 10 % and a maximum of almost 30 % (Figure 1). After 8-10 weeks however, the volumes had stabilized at a level hardly differing from their values at the start of the experiment, viz. at 97.5 ± 6.3 % of the initial volumes.

The overall mean shrinkage of the eggs, as calculated from the above measurements (≈ 2.5 %), was found to be statistically insignificant. Therefore, it was decided that no further corrections for the preservation effect were required, provided that the eggs were left in formalin for a period of at least two months.

The developmental stages of the eggs were identified using DE FIGUEIREDO and BARRACA's (1963) criteria for stages 1 and 2, and the eye diameter/egg diameter ratio for stages 3 and 4. The latter method was chosen for because DE FIGUEIREDO and

BARRACA's stages, which apply to fresh, non-preserved eggs, could not easily be recognized in preserved eggs. As a matter of fact formalin preservation was found to change both the colour and the appearance of the eggs, two criteria which are essential to DE FIGUEIREDO and BARRACA's key.

## 3. Results

### 3.1. Market sampling programme

The relative frequencies of berried and hatching females (as compared to the total number of females in the samples) over the period September 1986-June 1989 are given in Figure 2.

Figure 3 shows the relative frequencies of berried females in the size-classes 31-35, 36-40, 41-45 and 46-50 mm CL.

The percentages of males as compared to the total numbers of *Nephrops* in each size-class (also referred to as sex-ratios) are plotted in Figure 4.

### 3.2. Abdominal eggs

Figure 5 shows the relative frequencies of the successive developmental stages of the abdominal eggs, viz. stages 1-4 and hatching, presented in the form of a stacked bar chart.

During wintertime, when the berried females most efficiently hide in their burrows, the numbers of berried females in the samples usually were far too small to allow reliable calculations of these relative frequencies. This was the case in January-February 1987, January-March 1988 and January-April 1989 (cf. the blanks in Figure 5).

The monthly LPUEs (in numbers per hour fishing) of berried females carrying stage 1 and stage 4 eggs, and of hatching females are given in Figures 6-8.

These graphs too contain some blanks, corresponding to the months for which the data series were not sufficiently large.

All percentages were calculated from data converted to numbers per hour fishing, to minimize the effect of size related differences in sampling intensity (absolute sample size was constant throughout the investigations, actually meaning that the ratio between sample size and landed volume varied considerably from one length class to another).

## 4. Discussion

### 4.1. Market sampling programme

The results of the market sampling programme corroborate the findings of earlier investigations on the reproductive cycle and the seasonal behaviour of Nephrops in the Central North Sea (REDANT, 1987). Since most general features of the reproductive cycle already were discussed on that occasion, the present discussion has been limited to the data which depart from the general picture or which are essential to the interpretation of the abdominal egg data.

(a) As a rule spawning takes place in September-November and hatching in late spring and summer (Figure 2).

The reproductive cycle of 1987-88 however, was rather exceptional, amongst others with respect to the progress of the spawning season. In 1987 the percentage of berried females reached its maximum only in December, i.e. almost two months later than in the other years. This delay had no major effect on the further course of the reproductive cycle and hatching occurred within the normal period of the year in 1988 (viz. from April till August with peak values in May-July, Figure 2).

In addition, the peak value in the percentage of berried females at the height of the 1987 spawning season was clearly lower than in the other years. This seems to indicate that spawning was less successful in 1987 - at least in terms of relative numbers of spawning females - than in the previous and in the following years (cf. Figure 2 in this paper and Figure 1 in REDANT, 1987).

A similar conclusion can be drawn from the LPUEs for berried females carrying stage 1 eggs (Figure 6). These too were markedly lower in autumn 1987 than in 1986 or 1988.

(b) The course of the reproductive cycle is roughly similar in all size-classes of females (Figure 3).

Again, relatively large numbers of non-berried females were observed in the mid-winter samples (usually between 5 and 15 % of all Nephrops > 30 mm CL landed, with peak values exceeding 25 % in January-February 1988). This is in agreement with the results of the earlier investigations and confirms that not all sexually mature females spawn every year.

The same holds for another finding already reported, namely that the percentages of berried females at the height of the spawning season are inversely related to the size of the females (cf. the peak values for the different size-classes in December 1987 and in October 1988, Figure 3).

These observations allege supporting evidence to the hypothesis that the chances of remaining non-berried, and hence of skipping a reproduction cycle, increase with increasing size of the females.

(c) The sex-ratios of the landings show marked seasonal variations, due to sex and condition related differences in seasonal behaviour (Figure 4).

During wintertime, when most females are berried and much more actively hiding in their burrows than the males or the non-berried females, more than 80 % of the landings consist of males.

Immediately before the start of the spawning season however, when the females are as vulnerable to trawling as the males, the sex-ratios reach their lowest values. In this particular period of the year the observed sex-ratios can be considered as being the nearest possible approximation of the 'real' sex-ratios for each size-class, mainly because the bias due to the peculiar behaviour of the berried females is then minimal. These sex-ratios clearly increase with increasing body size, from only 20-40 % males in the 31-35 mm CL size-class to more than 95 % males in the > 50 mm CL size-class (cf. the sex-ratios in September 1987 and August 1988, Figure 4).

Once more the data for 1987-88 did not fully conform to the general pattern. As opposed to 1986 and 1988 the sex-ratios increased much more slowly after the beginning of the 1987 spawning season. Besides, they also remained much lower throughout the following winter.

This can only be explained by assuming that the non-berried females were far more abundant in autumn and winter 1987-88 than usual, an assumption which closely fits the conclusions advanced under para (a) on the success - or rather on the relative failure - of the 1987 spawning season.

## 4.2. Abdominal eggs

The development of the abdominal eggs can easily be read from the data in Figures 5-8. During and immediately after the spawning season nearly all females carry stage 1 eggs. From then onwards there is a gradual shift to the later stages, culminating in the predominance of stage 4 before and during the hatching season.

The main periods over which the successive developmental stages occur can be summarized as follows :

| | | | | |
|---|---|---|---|---|
| stage 1 | : | August | --> | December |
| stage 2 | : | November | --> | January |
| stage 3 | : | January | --> | May/June |
| stage 4 | : | March | --> | July |

These data fully agree with the results of the market sampling programme with respect to the course of the reproductive cycle, viz. spawning in September-November and hatching in April-August.

There are, however, a number of interesting exceptions to the general picture, which deserve closer examination.

On several occasions berried females carrying stage 1 or stage 4 eggs were observed distinctly outside the 'normal' periods. This was the case in March-May 1987, April-May 1988 and May 1989 for stage 1, and in November-December 1987 and November 1988 for stage 4 (Figures 6 and 7). More than half of these females were > 40 mm CL.

It is generally assumed that the reproductive cycle of Nephrops consists of a series of more or less synchronized events : moulting, mating, spawning, egg-bearing and hatching (see e.g. CONAN, 1978 ; BAILEY, 1984 ; REDANT, 1987 and this study). The above mentioned data however show that some females, for one reason or another, may get out of pace with the majority of the female population.

Most likely the females in question spawned rather late (cf. the berried females with stage 1 eggs in March-May), maybe because they recovered more slowly from moulting and ovary maturation (BAILEY, 1984).

As a result hatching will equally be delayed, to take place completely out of phase with the rest of the population (cf. the berried females with stage 4 eggs in November-December).

One can hardly imagine that these females, after having hatched in December or even later, still would participate in the ongoing reproduction cycle which, as far as mating and spawning is concerned, must be fully completed by then. It is much more likely that they will skip that year's spawning, thereby shifting from annual to biennial spawning.

Whether from then onwards they will pursue a biennial spawning regime or shift to an irregular alternation of annual and biennial spawning is not yet clear.

## 4. Conclusions

The results of the present investigations largely confirm the findings of earlier studies on the reproduction of Central North Sea Nephrops. They also produce additional evidence to the hypothesis of biennial spawning, even though the question on the continuity of such a spawning regime, once it started, still remains to be solved.

The fact however, that even within the smaller size-classes (viz. 31-35 and 36-40 mm CL) females were found to be out of rhythm with the majority of the female population, suggests that biennial spawning is not restricted to the largest size-classes of females.

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## Norway lobster
## Effect of formalin preservation on the volume of abdominal eggs

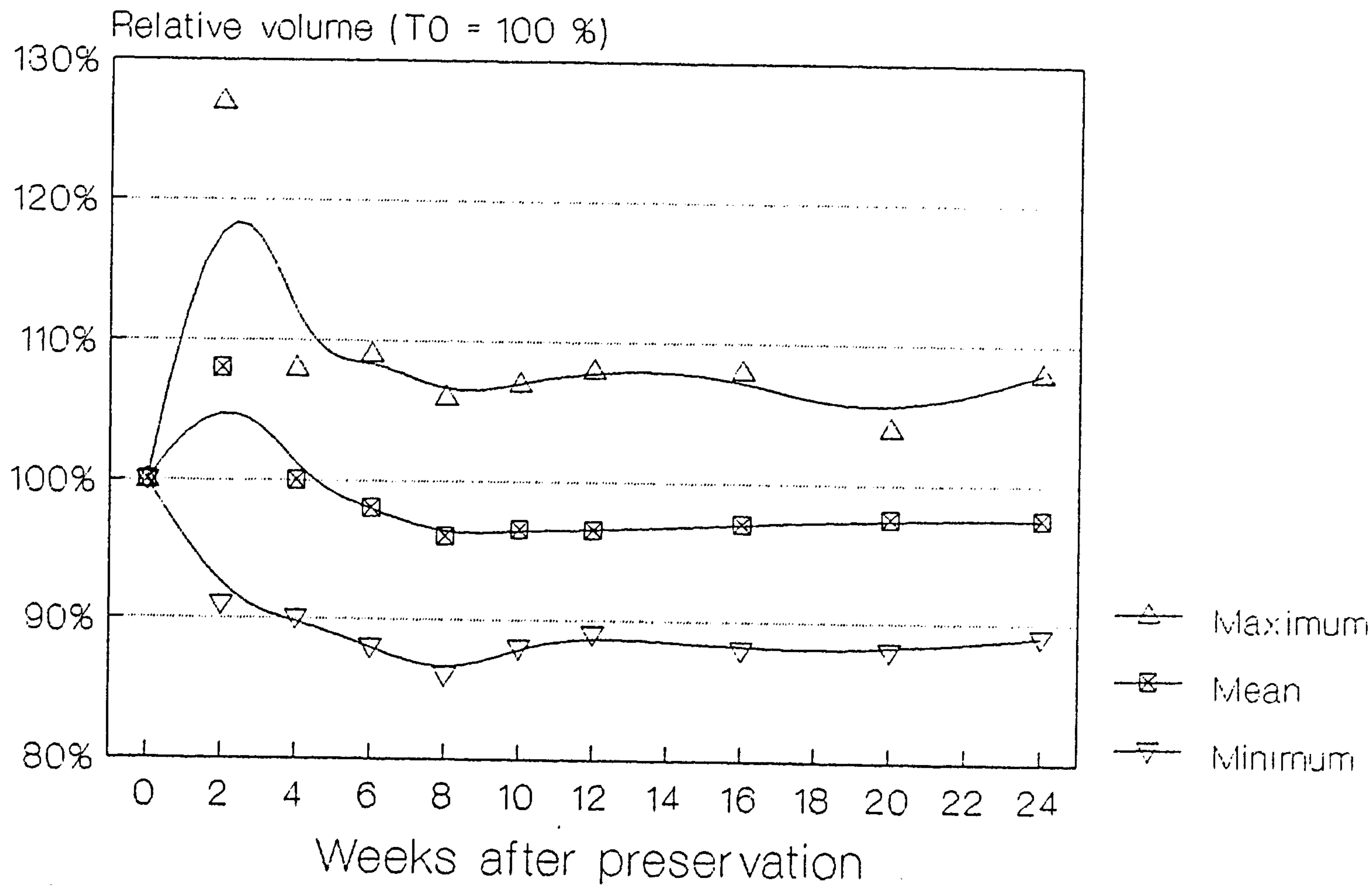
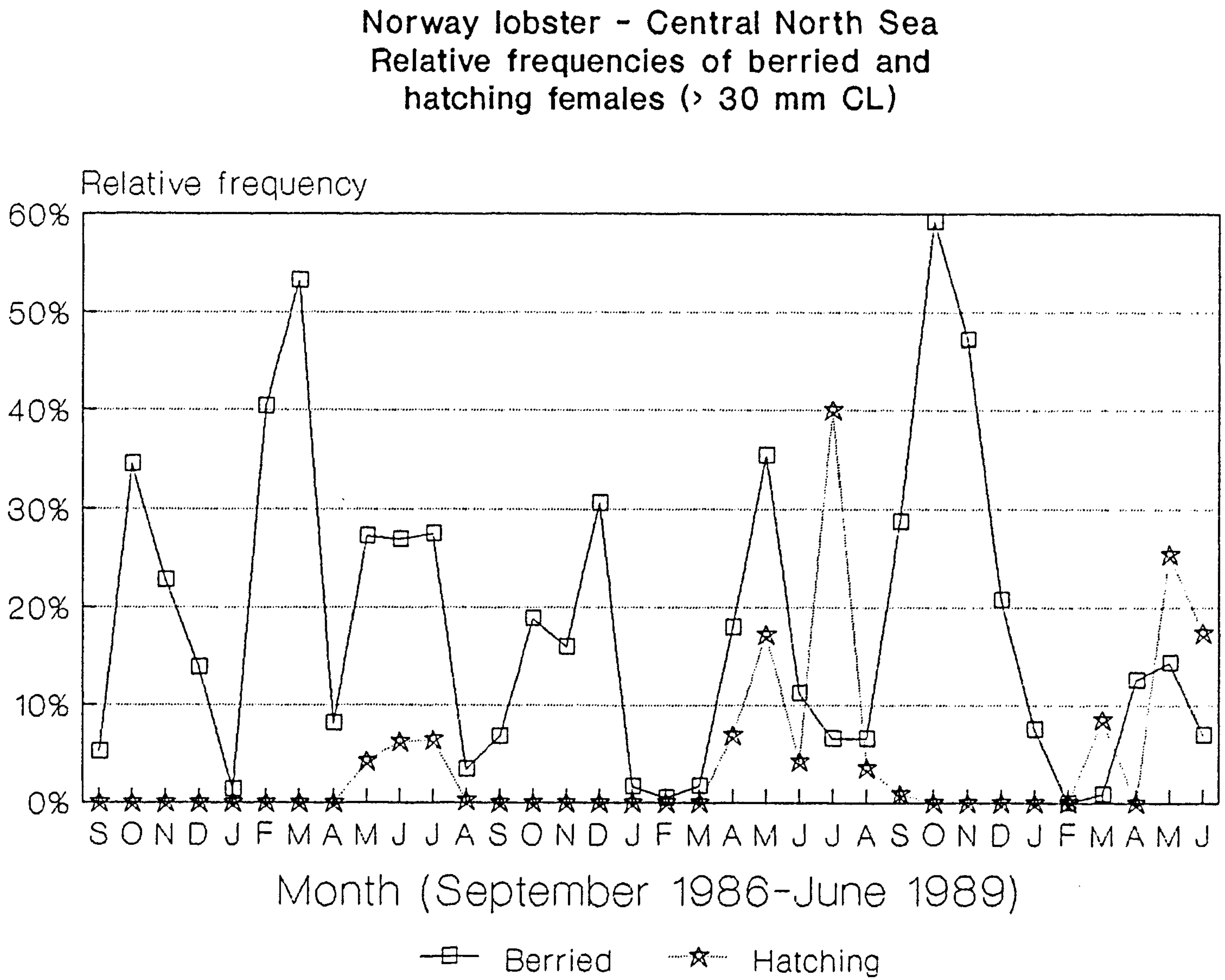



Figure 1



Norway lobster - Central North Sea
Relative frequencies of berried and hatching females (> 30 mm CL)
Relative frequency
60%
50%
40%
30%
20%
10%
0%
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
Berried
Hatching


Figure 2

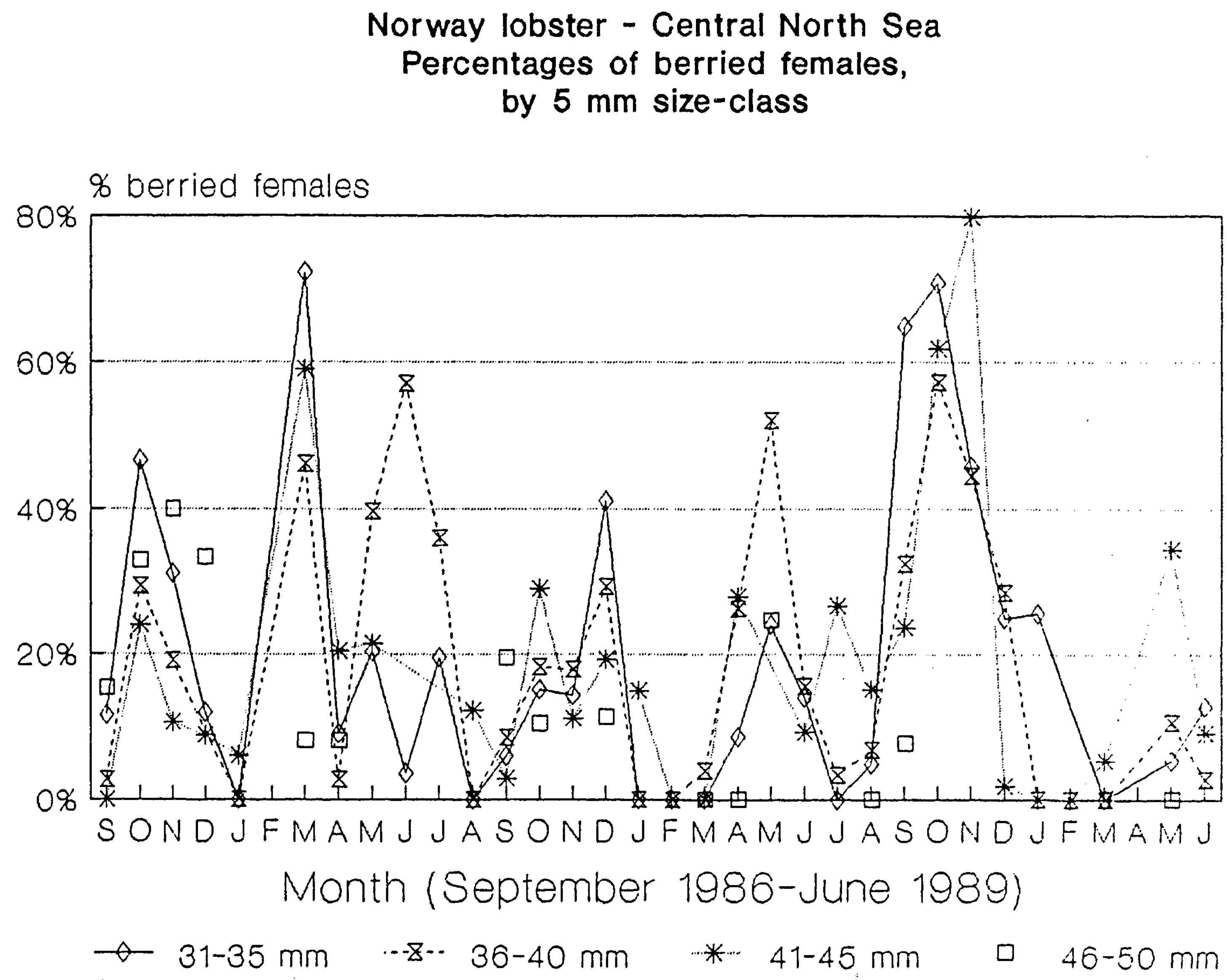

Norway lobster - Central North Sea
Percentages of berried females,
by 5 mm size-class
% berried females
80%
60%
40%
20%
0%
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
31-35 mm
36-40 mm
41-45 mm
46-50 mm

Figure 3

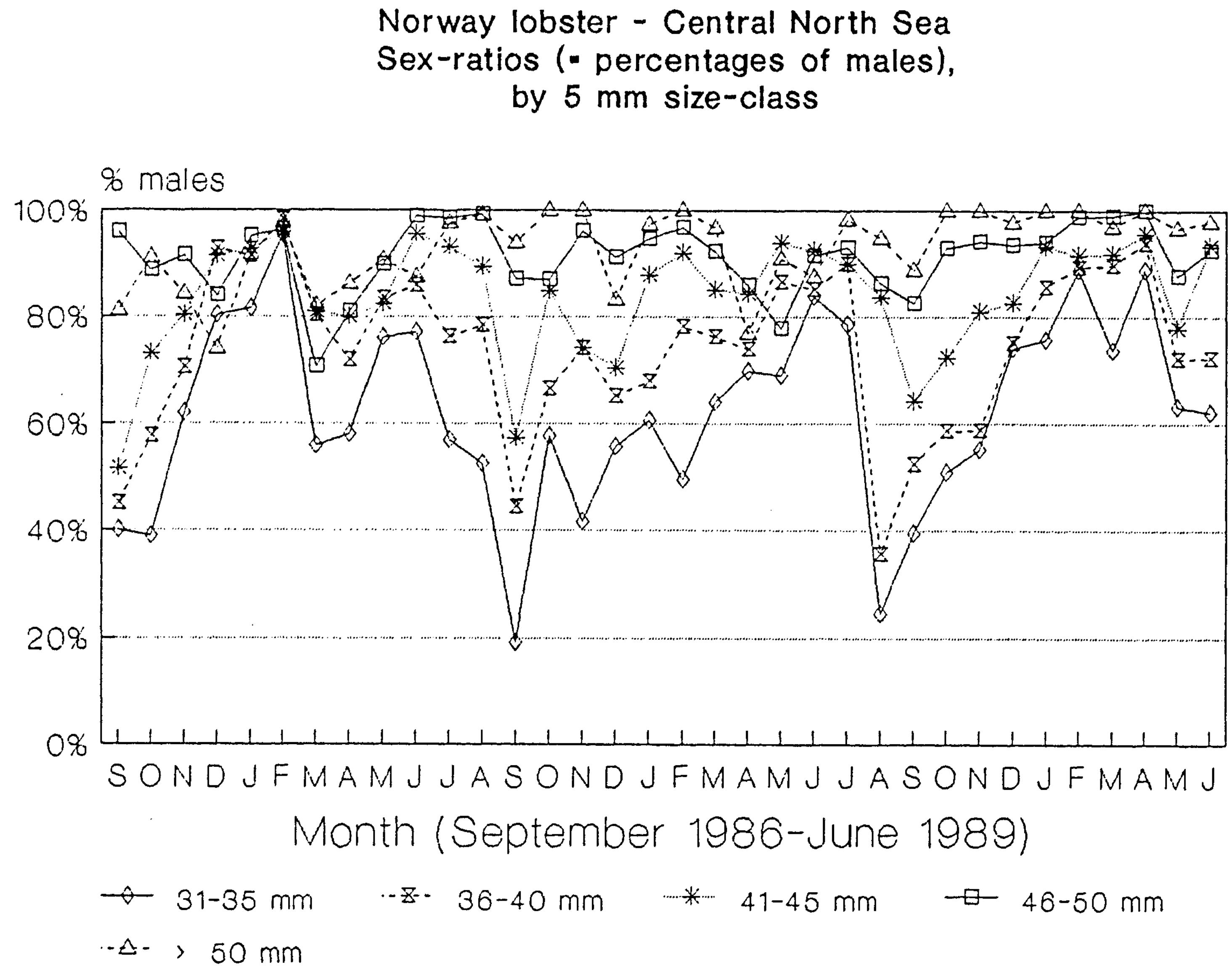

Norway lobster - Central North Sea
Sex-ratios (= percentages of males),
by 5 mm size-class
% males
100%
80%
60%
40%
20%
0%
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
31-35 mm
36-40 mm
41-45 mm
46-50 mm
> 50 mm

Figure 4

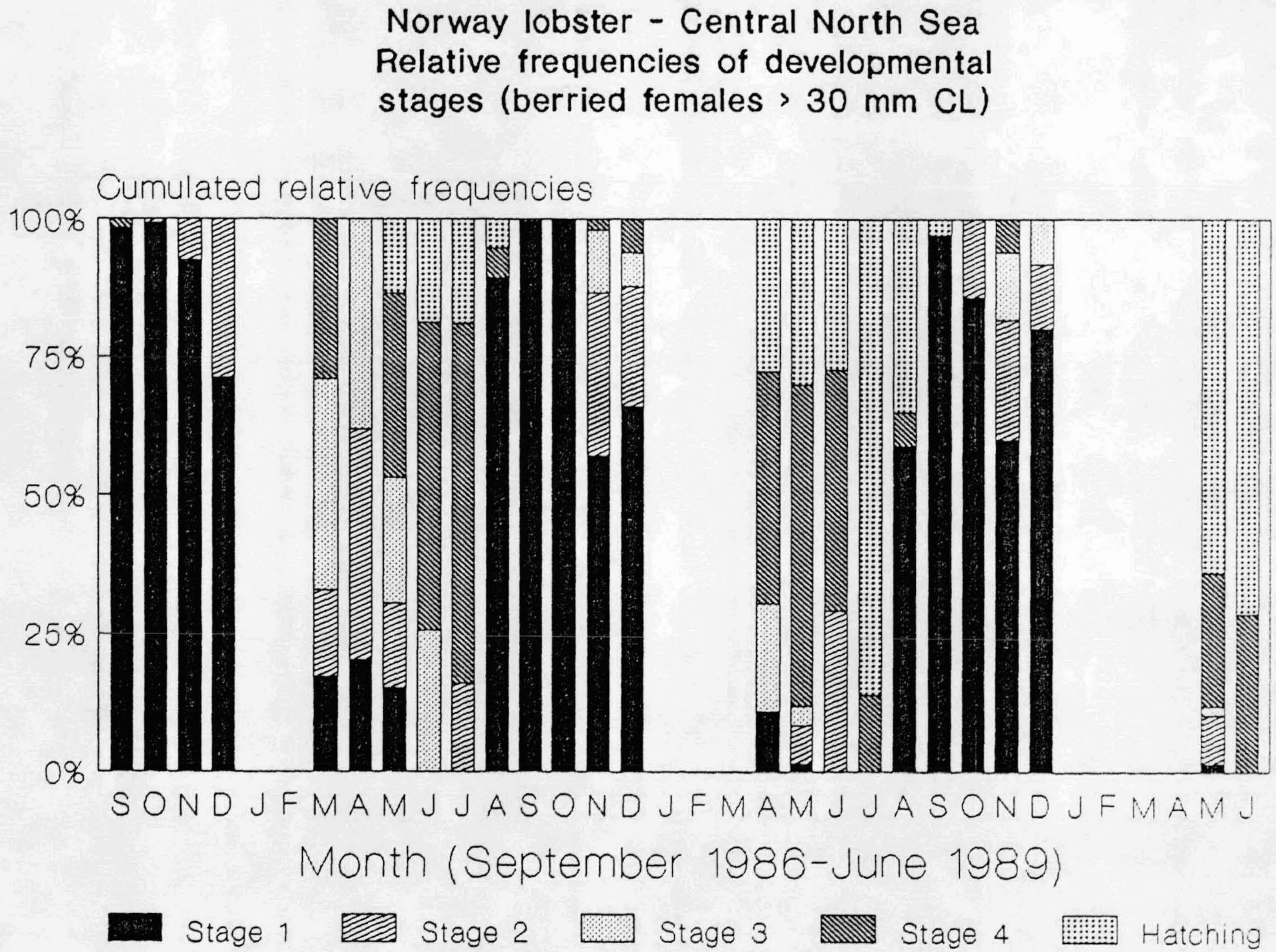

Norway lobster - Central North Sea
Relative frequencies of developmental stages (berried females › 30 mm CL)
Cumulated relative frequencies
100%
75%
50%
25%
0%
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
Stage 1
Stage 2
Stage 3
Stage 4
Hatching

Figure 5

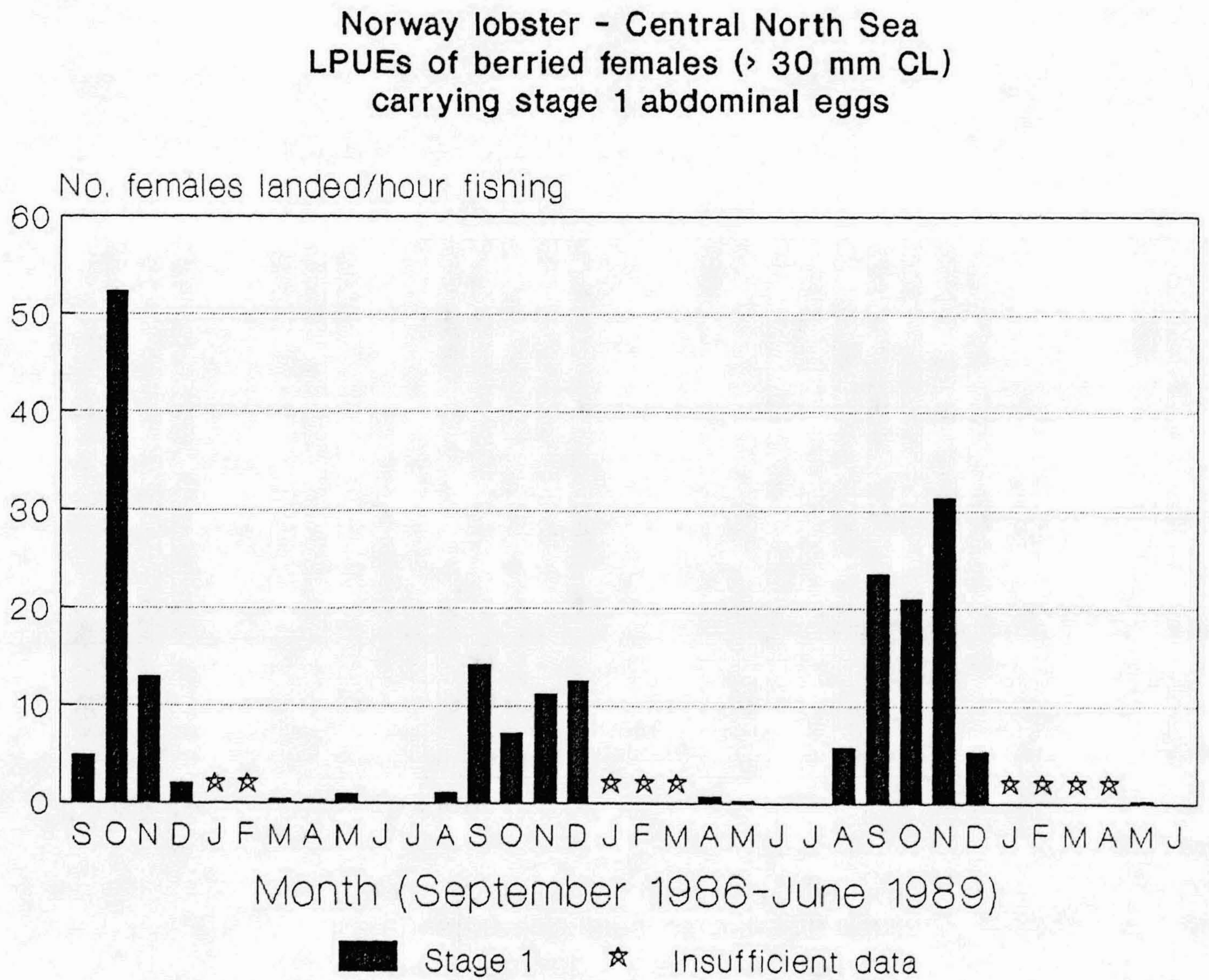

Norway lobster - Central North Sea
LPUEs of berried females (› 30 mm CL)
carrying stage 1 abdominal eggs
No. females landed/hour fishing
60
50
40
30
20
10
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
Stage 1
Insufficient data

Figure 6

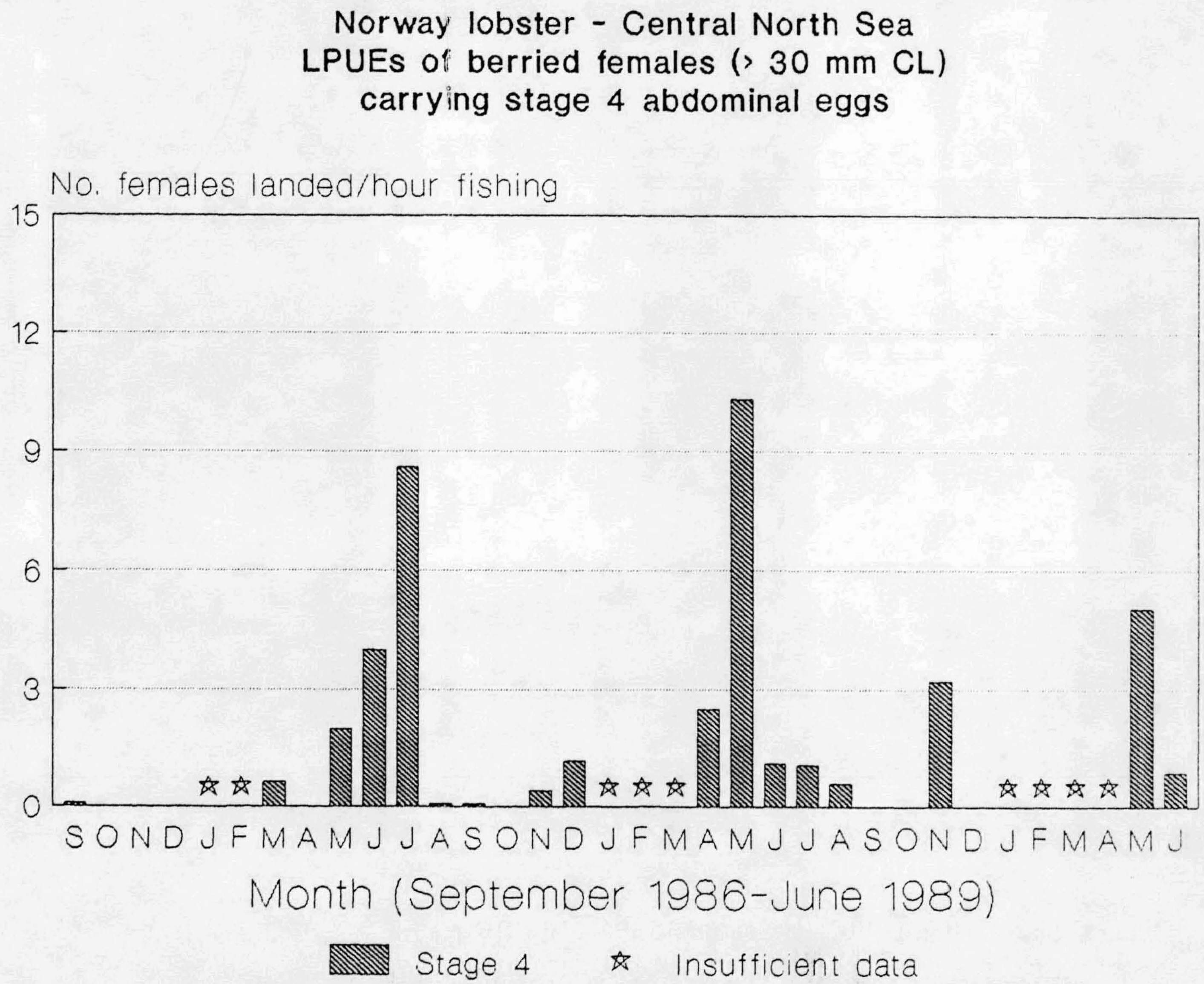

Norway lobster - Central North Sea
LPUEs of berried females (> 30 mm CL)
carrying stage 4 abdominal eggs
No. females landed/hour fishing
15
12
9
6
3
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
Stage 4
Insufficient data

Figure 7

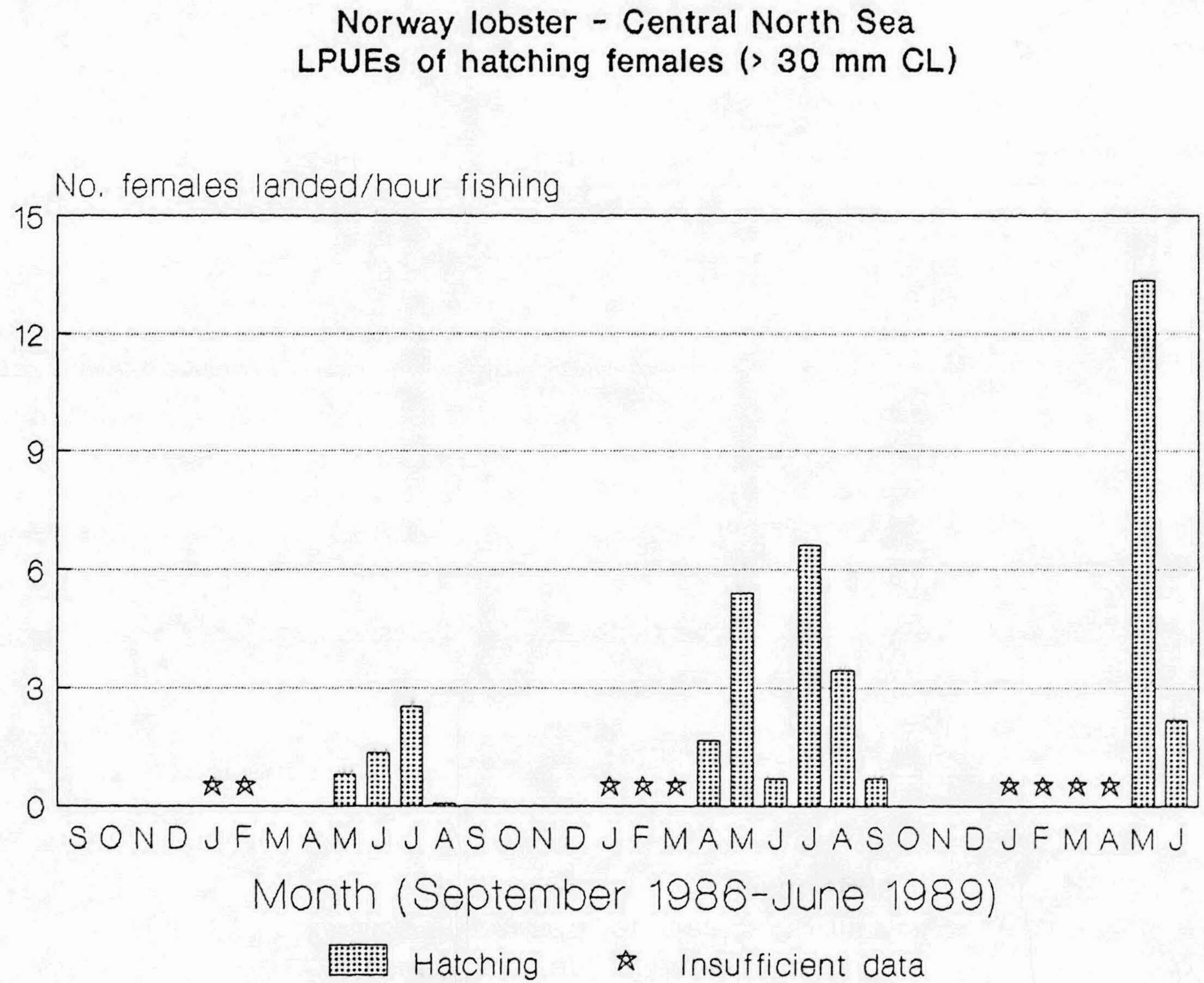

Norway lobster - Central North Sea
LPUEs of hatching females (> 30 mm CL)
No. females landed/hour fishing
15
12
9
6
3
0
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
Month (September 1986-June 1989)
Hatching
Insufficient data

Figure 8