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Reproduction and seasonal behaviour of the Norway lobster, Nephrops norvegicus, in the Central North Sea

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ABSTRACT

The reproductive cycle and the seasonal behaviour of the Norway lobster, Nephrops norvegicus, in the Central North Sea were studied through the analysis of market samples.

As a rule spawning takes place in September-October and hatching in April-June. The data on the relative abundance of non-berried females however suggest that, especially amongst the larger females, spawning might be biennial. The possible effect of abnormally low temperatures, particularly during winter-time, on the onset of biennial spawning is emphasized.

The landings per unit effort of the Nephrops fishery show a clear seasonal pattern, with maximum values during late spring, summer and early autumn, and minimum values during winter. These fluctuations can be attributed to the seasonal behaviour of male and female Nephrops in general and to the typical behaviour of the berried females, which hide most efficiently in their burrows throughout the egg-bearing period.

The study was subsidized by the Institute for Scientific Research in Industry and Agriculture (ISRIA), Brussels, Belgium.

The data on the sex-ratios of the Nephrops landings are discussed in relation to the reproductive cycle and the seasonal behaviour of both male and female Nephrops. During winter-time, when most of the females are berried and therefore less accessible to trawling than the males, more than 80 % of the landings are composed of males. During summer-time, when the females are as accessible to trawling as the males, the proportion of females in the landings may increase to more than 60 %, depending on the size of the Nephrops in question.

RESUME

Le cycle de reproduction et le comportement saisonnier de la langoustine, Nephrops norvegicus, dans la Mer du Nord centrale ont été étudiés par prélèvements des débarquements.

En général la ponte a lieu en septembre-octobre et l'éclosion des oeufs en avril-juin. Or, les données sur l'abondance relative des femelles non-ovigères suggèrent que la ponte pourrait être biennale, notamment parmi les femelles de plus grande taille. L'effet possible de températures anormalement basses, surtout en hiver, sur le déclanchement d'un régime de ponte biennale est souligné.

Les débarquements par unité d'effort de la pêche langoustinière varient d'une façon très nette au cours de l'année, avec des valeurs maximales à la fin du printemps, en été en au début de l'automne, et des valeurs minimales en hiver. Ces fluctuations peuvent être attribuées au comportement saisonnier des Nephrops mâles et femelles en général et au comportement particulier des femelles grainées, qui s'abritent très efficacement dans leurs terriers pendant la période d'incubation.

Les données sur les sex-ratios des débarquements de langoustines sont traitées par rapport au cycle de reproduction et par rapport au comportement saisonnier des Nephrops. En hiver, quand la plupart des femelles sont grainées et donc moins chalutables que les mâles, ceux-ci constituent plus que 80 % des débarquements. En été, quand les femelles sont aussi chalutables que les mâles, la proportion des femelles dans les captures peut dépasser les 60 %, selon la taille des langoustines en question.

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1. Introduction

Numerous investigations, especially during the last decades, have contributed to enhance our knowledge on the reproduction and the seasonal behaviour of the Norway lobster, Nephrops norvegicus, throughout its geographical range. Comprehensive reviews on this subject can be found in CHAPMAN (1980) and in the latest Reports of the ICES Nephrops Working Group (ICES, 1982, 1984).

In most Nephrops populations around Southern and Western Europe spawning appears to be annual, whereas around Iceland it is clearly biennial (KARLOVAC, 1953 ; FIGUEIREDO and BARRACA, 1963 ; EIRIKSSON, 1970 ; FARMER, 1974 ; CONAN, 1978). For North Sea Nephrops there is some evidence, albeit rather scanty, that not all sexually mature females spawn every year and that spawning might be biennial (ANDERSEN, 1962 ; SYMONDS, 1972). More recently BAILEY (1984), who studied the reproduction of Nephrops in the Clyde (W.-Scotland), found that female Nephrops may shift from annual to biennial spawning in relation to their size.

The present contribution discusses the results of a two years' study on the reproductive cycle of female Nephrops in the Central North Sea, the seasonal behaviour of male and female Nephrops, which in the case of the females is closely related to their egg-bearing condition, and the effect of reproduction and seasonal behaviour on the sex-ratio of the Nephrops landings.

2. Material and methods

Market samples were collected between April 1985 and March 1987 from the landings of commercial Nephrops trawlers fishing in the Botney Gut - Silver Pit area (Central North Sea). Sampling took place at approximately fortnightly intervals, mostly at the fish-auction of Zeebruges.

Currently the landings of Belgian Nephrops trawlers are marketed in three size classes : "small" ($\leq$35 mm carapace length), "medium" (30-45 mm carapace length) and "large" ($>$35 mm carapace length). From each size class 100 Nephrops were taken for analysis in the laboratory. Measurements included carapace length (to the nearest 0.5 mm), sex and reproductive state of the females (non-berried, berried or with remains of recently hatched eggs between the pleopods).

During the investigations however it appeared that only part of the smallest Nephrops in the catches are actually landed. Very often only those from the last hauls are kept for marketing, the others being discarded at sea, and in some cases even none

of them are landed at all. Since the relation between the total volume of small Nephrops caught and the quantities actually landed was unknown or at least uncertain it was impossible to estimate the composition of the catches as a whole, by pooling the data for the three market classes. Therefore only the data for the size classes "medium" and "large", for which this particular problem did not arise, were considered in the present study.

Monthly averages of the proportions of berried females and of females with egg-remains (both expressed as a percentage of the total number of females), the landings per unit effort (in numbers of Nephrops landed per hour fishing) and the sex-ratio of the landings (given as the percentage of males) were calculated per 5 mm length class and for all length classes combined, taking into account the relations between sample weight and total volume of the landings.

3. Results and discussion

3.1. Reproductive cycle

The seasonal fluctuations in the proportions of egg-bearing females and of females with remains of recently hatched eggs are given in Figure 1 for all length classes >30 mm carapace length combined, and in Figure 2 per 5 mm length class.

Spawning takes place in September-October, as shown by the sharp rise in the percentage of berried females from less than 10 % in late summer to 35-60 % in autumn (Figure 1). Shortly afterwards the percentage of berried females drops to much lower values, to reach a minimum in January-February. This corresponds to the period during which the berried females hide in their burrows, thus making them less accessible to trawling than the non-berried females or the males. Although this behavioural pattern is a common feature of both male and female Nephrops (see section 3.2.) it is much more pronounced amongst the berried females than amongst the non-berried females and the males (FIGUEIREDO and THOMAS, 1967).

By the end of the winter the egg-bearing females start to leave their burrows much more frequently, which results in a short-term rise of the proportion of berried females in the landings. From April-May onwards their percentage decreases again, mainly because the eggs, which are by now fully developed, start to hatch. This is confirmed by the occurrence of relatively large numbers (10-25 %) of females with remains of recently hatched eggs in late spring and early summer. The hatching process is completed by midsummer.

The incubation of the eggs (i.e. the space of time between spawning in September-October and hatching in April-June) thus takes about 9 months.

Shortly after hatching the females moult, in preparation of mating and subsequent spawning (THOMAS, 1965 ; FARMER, 1974 ; CONAN, 1978 ; BAILEY, 1984). Due to the current discarding practice on the Belgian Nephrops trawlers (usually the soft-shelled Nephrops are discarded upon capture or landed tails only) it was impossible to obtain reliable data on the occurrence of soft females from the market samples and, consequently, to identify exactly the period during which the post-hatching moult takes place. However, from the timing of the hatching period it could be inferred that most of the females which were berried during the previous winter moult in June-August.

These results are in line with the findings for other Nephrops stocks at similar latitudes, such as in the Danish waters, the Irish Sea and around Scotland (POULSEN, 1946 ; THOMAS, 1960 ; O'RIORDAN, 1961 ; THOMAS and FIGUEIREDO, 1965 ; FARMER, 1974 ; BAILEY, 1984 ; BAILEY et all., 1986).

Splitting the data of the percentages of berried females in 5 mm length classes showed that the course of the reproductive cycle is roughly similar in all length classes (Figure 2).

The fact however that even in midwinter relatively large numbers of non-berried females were observed in the landings (5-10 % of all Nephrops >30 mm carapace length landed) indicates that not all sexually mature females spawn every year. Most likely the females in question hatched rather late, so that they moulted only by the end of the summer and hence missed out that year's mating and spawning period.

This phenomenon seems to occur more frequently with increasing size of the females. The peak values in the percentages of berried females in September-October appear to be inversely related to the size of the females, the highest values being observed in the smallest length classes (Figure 2). This would actually mean that when the females grow older or bigger (from the data available in this study it is not evident whether this process is age - or size dependent) their chances to skip a spawning period would gradually increase, and that eventually they may shift from an annual to a biennial spawning regime or to a more or less regular succession of annual and biennial egg-bearing.

Similar spawning regimes have also been reported by ANDERSEN (1962) and SYMONDS (1972) for the Nephrops populations around the Faeroer and in the Farne Deeps, and more recently by BAILEY (1984), who observed almost identical features in the spawning periodicity of Nephrops in the Clyde.

As far as spawning frequency is concerned the Nephrops stock in the Botney Gut - Silver Pit area seems to be "transitional" between the Nephrops stocks in more southern areas (Irish Sea, Bay of Biscay, Portuguese waters, Mediterranean), where annual spawning appears to be the rule (KARLOVAC, 1953 ; FIGUEIREDO and BARRACA, 1963 ; FARMER, 1974 ; CONAN, 1978), and those in more northern areas (Icelandic waters), where spawning is clearly biennial (EIRIKSSON, 1970).

It is tempting to relate spawning frequency to temperature and in general this seems to be the case indeed. Observations under both natural and experimental conditions showed that the length of the incubation period is inversely related to the ambient temperature (DUNTHORN, 1967 ; CHAPMAN, 1980). At high temperatures the incubation period is relatively short (6-8 months), thus leaving sufficient time for the reproductive cycle to be completed within one year. Conversely, at low temperatures hatching may be delayed to such an extent that the females do not moult in time to take part in the current year's mating and spawning process, and that spawning becomes biennial.

The latter is obviously the case around Iceland and in some parts of the Faeroese waters, where the incubation of the eggs takes as long as 12 months (ANDERSEN, 1962 ; EIRIKSSON, 1970). It may also be the case in more temperate areas, such as e.g. in the North Sea or around Scotland, in the event of a severe winter. This suggests that the temperature at the sea-bed, especially during winter-time, could be a crucial factor in the relative success (or failure) of Nephrops recruitment and may explain at least partly the relationship between Nephrops catches per unit effort and temperature 3-6 years earlier, as reported by CHAPMAN (1984).

The findings of BAILEY (1984) on the reproductive cycle of Nephrops in the Sound of Jura and the Clyde however indicate that temperature is not the only factor determining spawning frequency. In populations with a high growth rate, resulting in size compositions containing large females, the increasing size of the females appears to retard recovery from moulting, maturation of the ovaries and, consequently, their availability for mating and spawning. Hence the growth rate of the females as such, which is governed by several environmental factors, including not only temperature but also food availability and competition, could play an important part in the onset of biennial spawning (BAILEY, 1984).

3.2. Seasonal behaviour

Monthly average landings per unit effort (LPUE's), in numbers of Nephrops landed per hour fishing, are given in Figure 3 for all length classes >30 mm carapace length pooled, and in Fi-

gures 4 and 5 for males and females separately, per 5 mm length class.

Within some confines these data can be considered as a measure of the relative abundance of Nephrops on the sea-bed and, accordingly, as a reflection of their seasonal behaviour.

In connection to this it should be noted that the LPUE-values for the winter months underestimate the actual availability of Nephrops. During winter-time the catches of Nephrops usually are very poor and therefore only part of the fishing effort in the Botney Gut - Silver Pit area is directed on Nephrops, the other part being directed on finfish in shallower parts of the area or on adjacent fishing grounds (i.e. in areas where Nephrops is ultimately scarce or even completely absent). The effort statistics however do not distinguish between fishing hours "on Nephrops" and fishing hours "on finfish". Consequently the LPUE-values, which were obtained by dividing the numbers of Nephrops landed by the total number of fishing hours, underestimate the actual availability of Nephrops on the Nephrops grounds.

In the period of peak catches, on the other hand, most of the effort is directed on Nephrops, except for a few occassional hauls on finfish, usually around midnight or by the end of the fishing trip (REDANT and DE CLERCK, 1984). Therefore in these months the effect of blending the effort data on the LPUE-values can be considered as being negligible.

The landings per unit effort for all size classes combined (Figure 3) show a clear seasonal pattern, with maximum values during late spring, summer and early autumn, and minimum values during winter.

Such fluctuations are a well known feature in the Nephrops fisheries all around Europe and are currently related to seasonal changes in the burrowing behaviour of Nephrops. During winter both males and females actively hide in their burrows, thus making them less accessible to trawling than during summer, when they emerge from their burrows more frequently and for longer periods of time (FIGUEIREDO and THOMAS, 1967 ; DUNTHORN, 1967 ; EIRIKSSON, 1968 ; CONAN, 1978).

As already stated this behavioural pattern is much more pronounced amongst the berried females than amongst the males and the non-berried females (see section 3.1.). Moreover, the berried females find their burrows earlier and leave them later in the year than the non-berried females, depending on the duration of the egg-bearing condition. This explains why the LPUE-values for the females as a whole rise later and drop off earlier and somewhat faster than those for the males (Figure 3).

Seasonal fluctuations in the catches or landings per unit effort, similar to those observed in the Central North Sea, have been reported for several other Nephrops stocks, such as in the

Scottish waters, the Celtic Sea, the Porcupine Bank, off North Galicia, off Portugal and in the Adriatic, although in this area the period of peak catches is 2-3 months earlier than in the North Sea (FROGLIA, 1972 ; ARROBAS, 1982 ; CHARUAU et all., 1982 ; FERNANDEZ, unpubl. data in ICES, 1984 ; BAILEY et all., 1986).

Also in this case there is no evidence of size related differences (Figures 4 and 5), effectively meaning that the behavioural pattern of all size classes of Nephrops > 30 mm carapace length is roughly the same.

One particular aspect in the periodicity of the LPUE-values deserves further attention. In July-August there appears to be a short-term but distinct drop in the LPUE-values (Figures 3, 4 and 5), a feature which is also seen in the catch per unit effort data for the Nephrops fleet as a whole (REDANT and DE CLERCK, 1984).

Most likely this drop in the LPUE-values is associated with the summer moult of male and female Nephrops (see also section 3.1.), whether because the soft-shelled animals are discarded at sea, or because the Nephrops hide in their burrows while moulting. In both cases the landings per unit effort would temporarily decrease.

Several other hypotheses have also been tested to explain this phenomenon, such as a shift of the Nephrops fleet from one part of the area at the beginning of the main Nephrops season to another part by the end of the season, misreporting of the landings in the period of peak catches or seasonal changes in the diurnal activity rhythm of Nephrops. All these hypotheses however could be rejected by negative evidence.

In contrast with the adult females, which moult only once per year, the adult males moult one to three times per year, depending on their age and size (FARMER, 1973 ; CONAN, 1978). Therefore we would expect to see similar drops in the LPUE-values for the males in other months too, provided that moulting is a synchronized process, as suggested by CONAN (1978), and not a succession of singular events, scattered over a long period of time. These drops however may be masked by the major changes in catchability, especially in spring and autumn, although there are some indications of a short-term drop in the LPUE-values in November-December, maybe corresponding to an early winter moult (Figure 4).

3.3. Sex-ratio of the landings

Data on the seasonal fluctuations in the sex-ratios of the landings (market classes "medium" and "large") are given in Figure 6.

These fluctuations are the combined result of sex related differences in seasonal behaviour (viz. of the berried females as opposed to the non-berried females and the males), growth rate and mortality.

In winter-time, when most females are egg-bearing and actively hiding in their burrows, the sex-ratios are maximal, more than 80 % of the Nephrops landings being composed of males. In summer-time, on the other hand, when most females are as accessible to trawling as the males, the sex-ratios show a remarkable drop, the extent of which is related to the proportion of males and females in each length class. These proportions are determined by the male/female-ratio at birth and, subsequently, by the differences in growth rate and instantaneous mortality between males and females (BAILEY, 1984). The decrease of the sex-ratios in spring and the subsequent increase in autumn correspond to resp. the hatching and the spawning period (see also section 3.1.).

In March-April there is another, smaller drop in the sex-ratios, corresponding to the sudden increase in the percentage of egg-bearing females in the landings already mentioned in section 3.1.

Similar seasonal fluctuations in the sex-ratios of catches or landings have been reported by THOMAS and FIGUEIREDO (1965) for the Scottish waters, by BRIGGS (unpubl. data in ICES, 1984) for the Irish Sea and by FIGUEIREDO (unpubl. data in ICES, 1984) for the Portuguese waters.

Although there is a vast amount of data on the sex-ratios of Nephrops catches and/or landings (for extensive reviews see e.g. ICES, 1982, 1984) it is very difficult to compare these data, except in a few cases where the similarities or differences are evident. Mostly however the data in the literature refer to catches or landings as a whole, i.e. to a mixture of length classes, whose range varies according to the actual composition of the population, the selective properties of the fishing gear used and, in the case of the landings, the discarding practice of the fishermen. Since in most Nephrops stocks there is a clear relationship between size and sex-ratio (see e.g. KARLOVAC, 1953 ; THOMAS, 1960 ; THOMAS and FIGUEIREDO, 1965 ; ALONSO-ALLENDE, 1976 ; SARDA and FERNANDEZ, 1981 ; ARROBAS, 1982 ; ICES, 1982, 1984) it is obvious that the range of length classes and their relative abundance in the catches or landings will strongly influence the sex-ratio.

4. Conclusions

The results of the present study are corroborative to the con-

clusions of ANDERSEN (1962), SYMONDS (1972) and BAILEY (1984) on the spawning frequency of female Nephrops in and around the North Sea. Especially for the large females there is growing evidence of biennial spawning, or at least of a more or less regular alternation of annual and biennial egg-bearing. The role of the increasing size of the females in their shifting from annual to biennial spawning seems to be confirmed. Nevertheless the potential effect of abnormally low temperatures, particularly during winter-time, on the onset of biennial spawning and the possible subsequent failure of Nephrops recruitment should be reckoned with.

The investigations also emphasize, once more, that each Nephrops stock may have its own biological peculiarities, including population structure, sex-ratio, reproductive cycle and seasonal behaviour, and that a thorough knowledge of these peculiarities is essential to understand stock to stock differences in exploitation pattern and catch composition, and, as a matter of evidence, to understand the management requirements of each stock.

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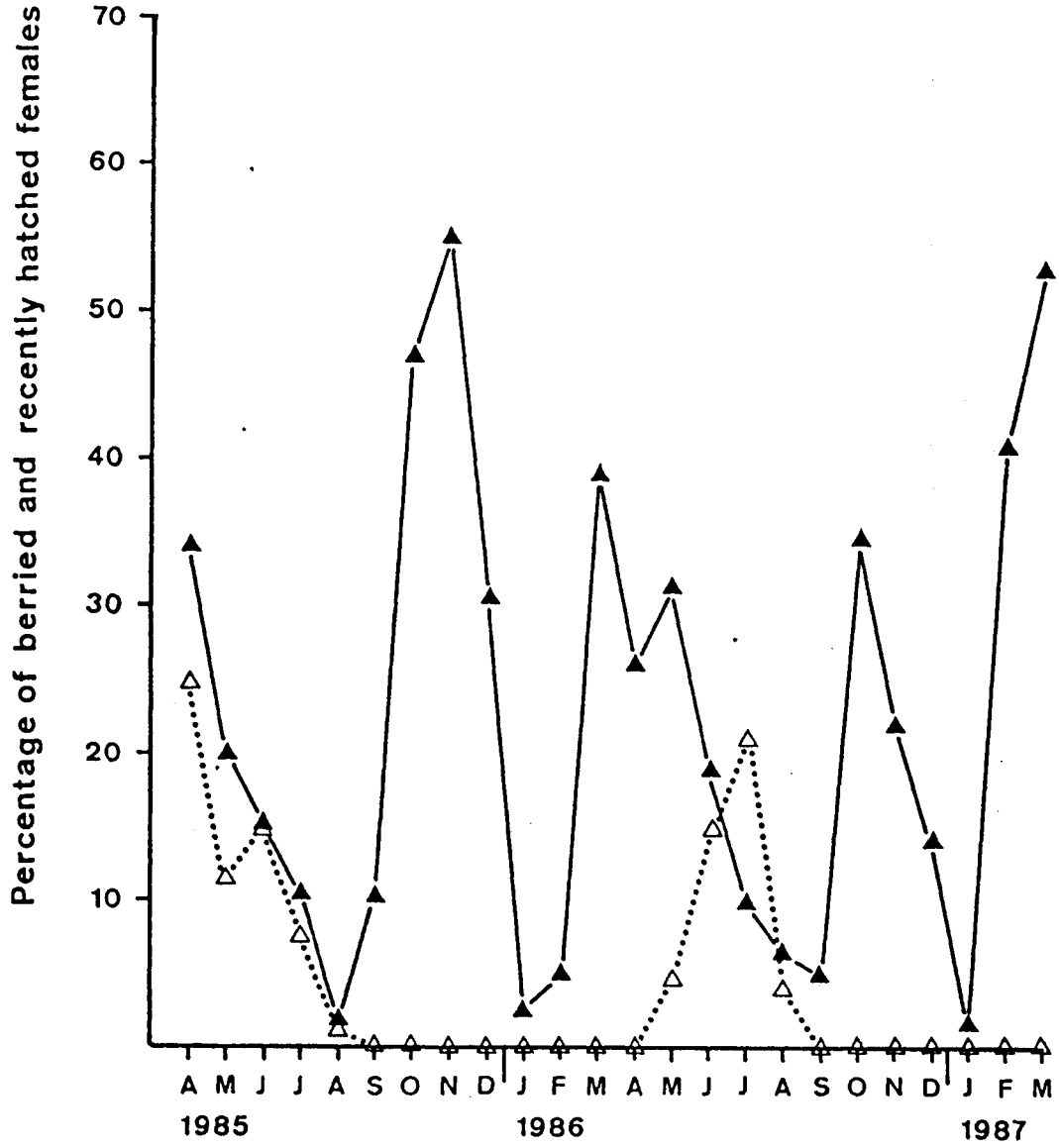

Figure 1 - Proportions of berried and recently hatched females (as a percentage of the total number of females) in the landings of Nephrops >30 mm carapace length, all size classes combined.

▲ : berried females
△ : recently hatched females

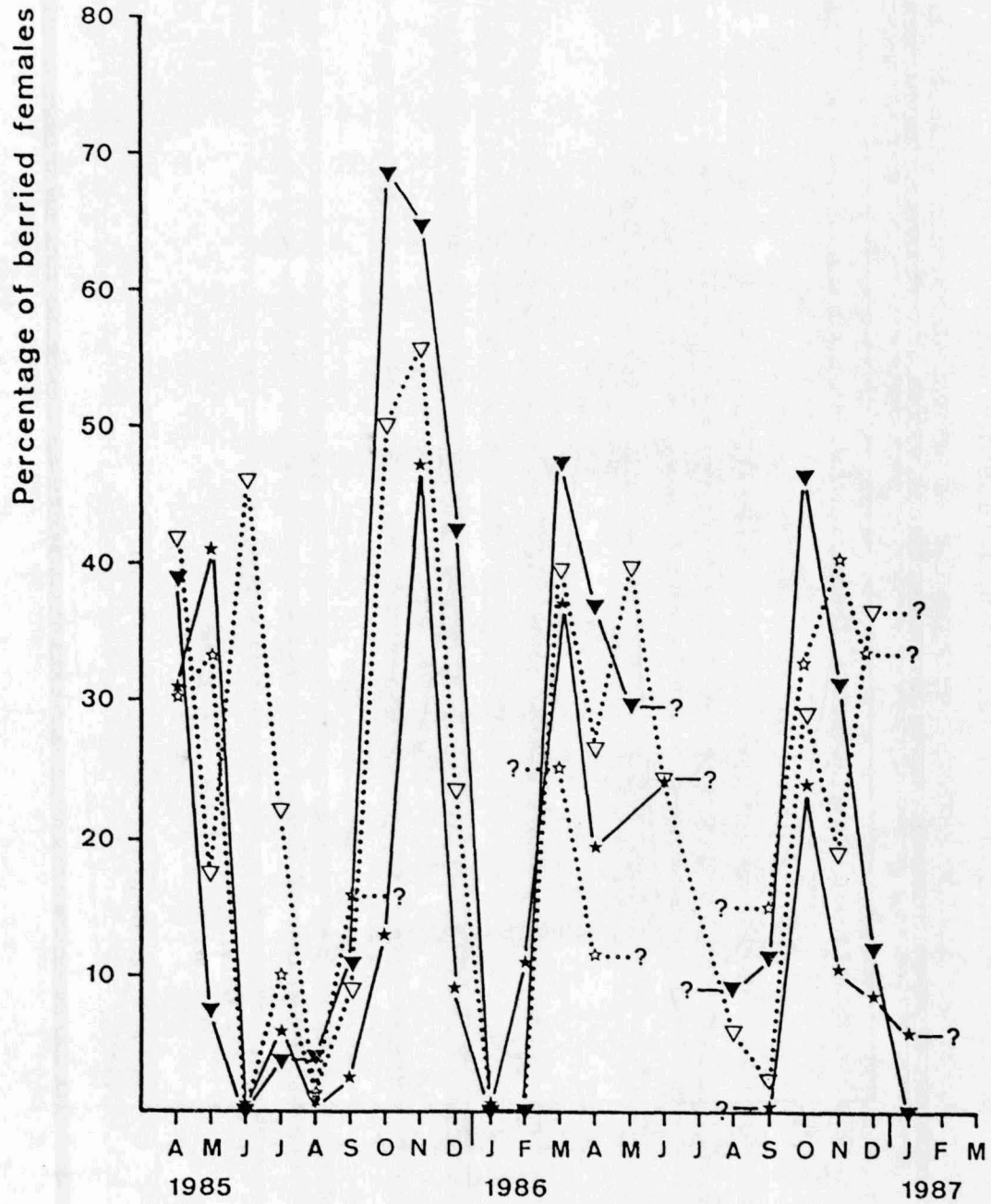

Figure 2 - Proportions of berried females (as a percentage of the total number of females) in the landings of Nephrops >30 mm carapace length, per 5 mm length class.

▼ : 31-35 mm carapace length
▽ : 36-40 mm
★ : 41-45 mm
☆ : 46-50 mm

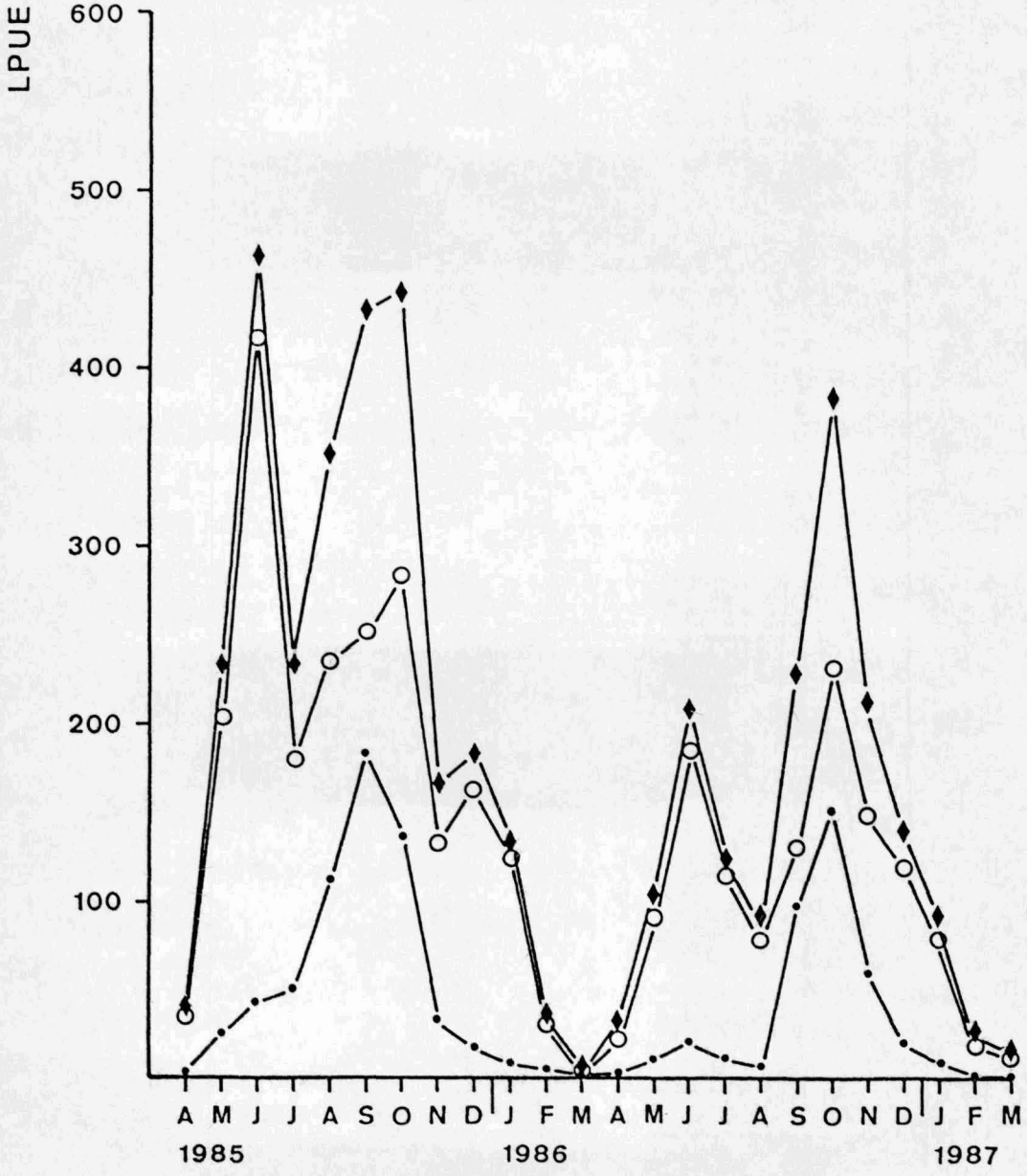

Figure 3 - Landings per unit effort (in numbers of Nephrops landed per hour fishing) of male and female Nephrops > 30 mm carapace length, all size classes combined.

○ : males
• : females
♦ : total Nephrops

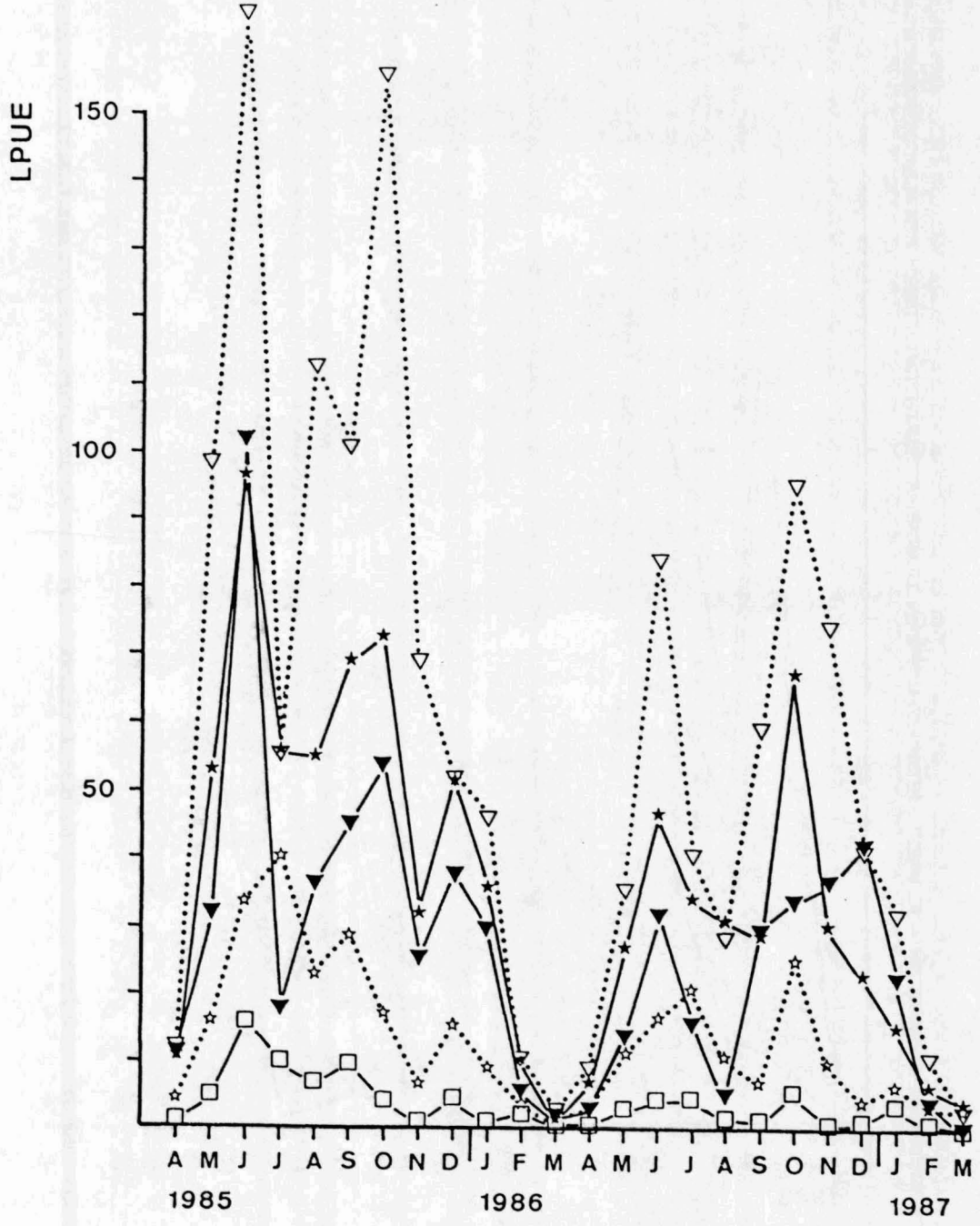

Figure 4 - Landings per unit effort (in numbers of Nephrops landed per hour fishing) of male Nephrops >30 mm carapace length, per 5 mm length class.

▼ : 31-35 mm carapace length
▽ : 36-40 mm
★ : 41-45 mm
☆ : 46-50 mm
□ : ⩾ 51 mm

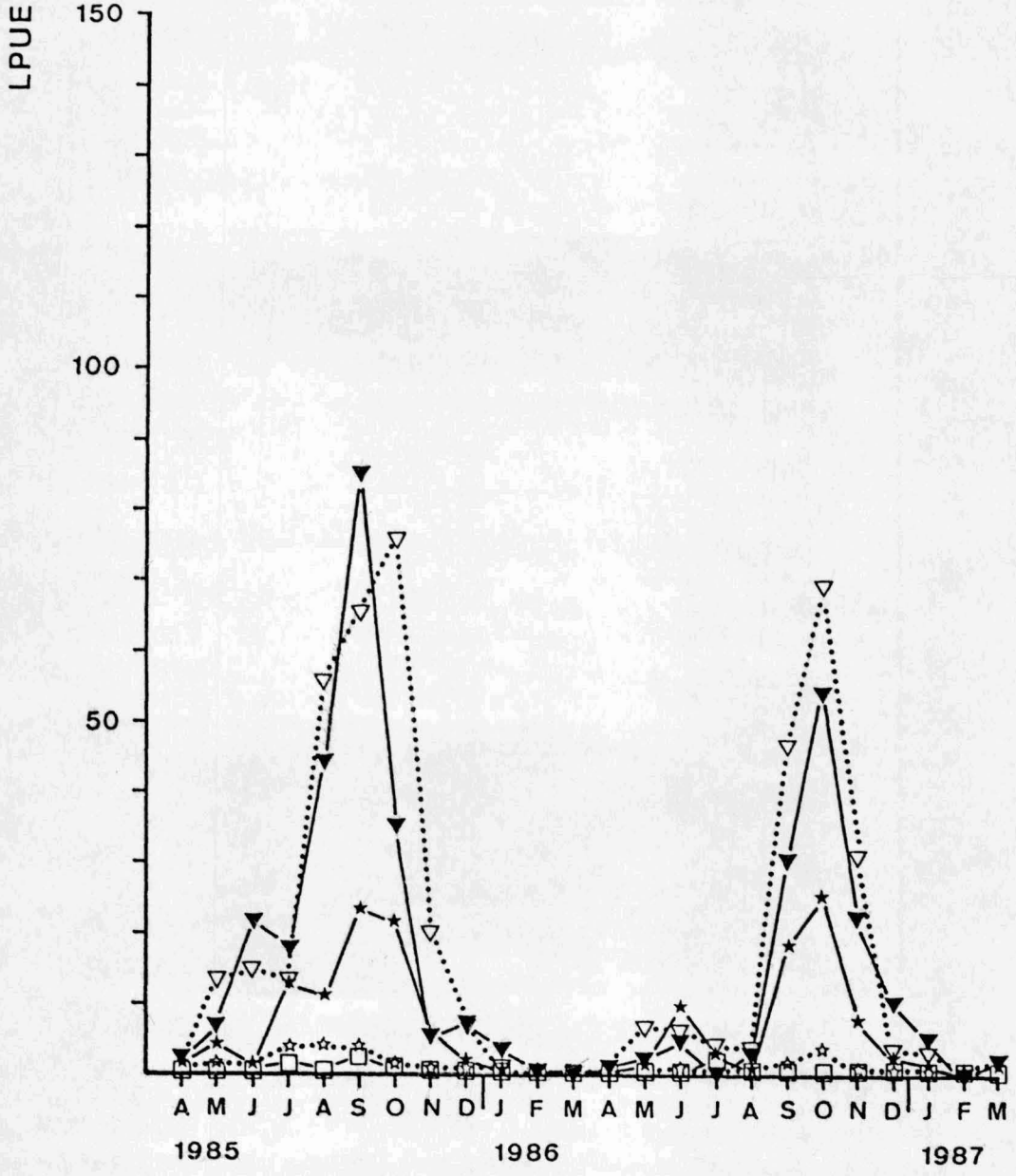

Figure 5 - Landings per unit effort (in numbers of Nephrops landed per hour fishing) of female Nephrops >30 mm carapace length, per 5 mm length class.

▼ : 31-35 mm carapace length
▽ : 36-40 mm
★ : 41-45 mm
☆ : 46-50 mm
□ : ⩾ 51 mm

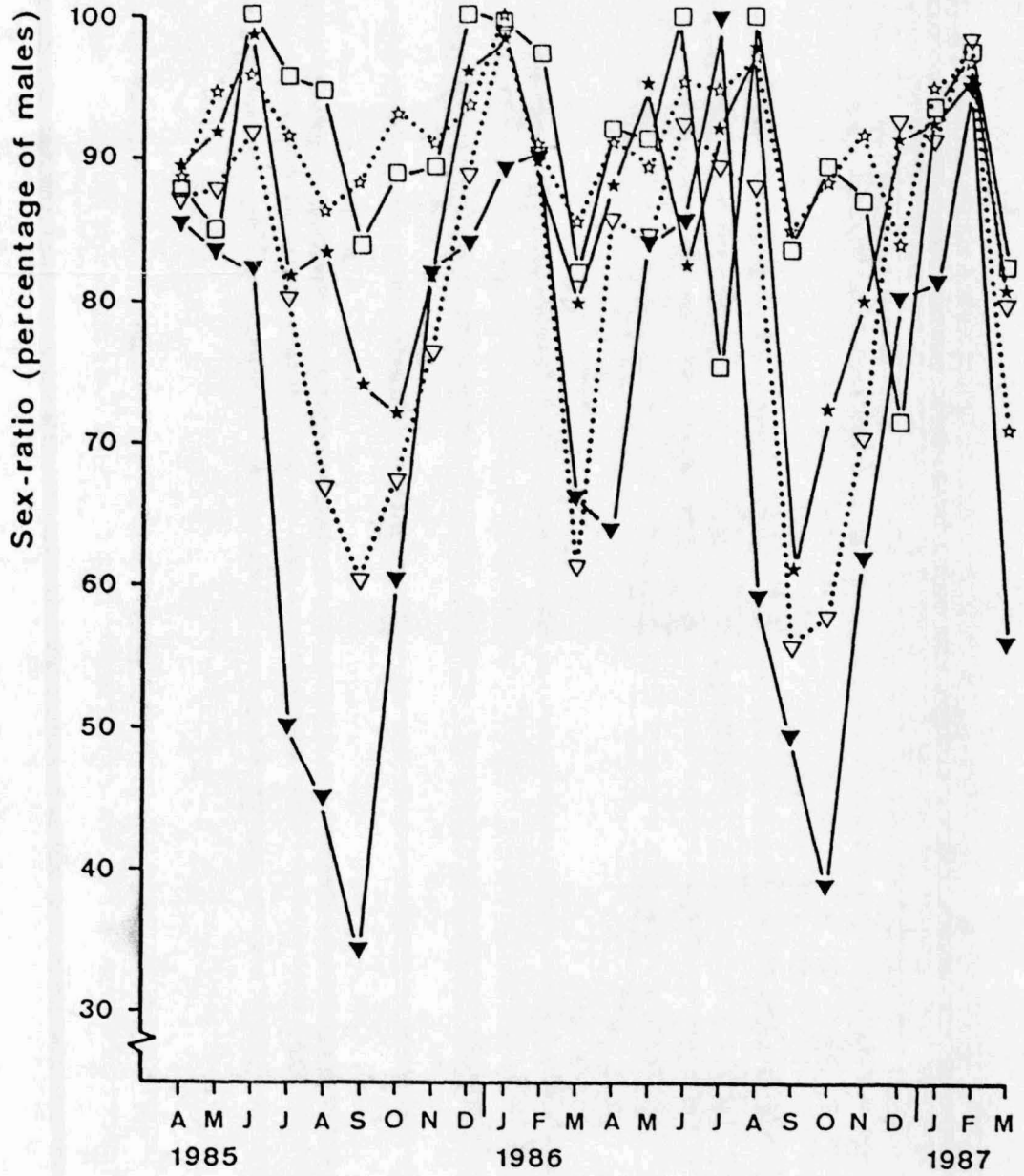

Figure 6 - Sex-ratios (given as the percentages of males) of the Nephrops landings > 30 mm carapace length, per 5 mm length class.

▼ : 31-35 mm carapace length
▽ : 36-40 mm
★ : 41-45 mm
☆ : 46-50 mm
□ : ⩾ 51 mm