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Protandric hermaphroditism in the brown shrimp, *Crangon crangon* (L.), and its effects on recruitment and reproductive potential

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ABSTRACT

The paper describes the results of histological investigations on the sex change of male brown shrimps, *Crangon crangon* (L.), and discusses its effects on recruitment and reproductive potential of the shrimp population in the Belgian coastal area. The percentage of males (length range 41-50 mm) with developing oocytes in the testes varied between 2.5-3.0 % in August and in October, and 9.2 % in September. Data on the sex-ratio of the shrimp population are presented and are analysed in relation to the possible occurrence of sex reversal. Estimates of the possible effect of sex reversal on recruitment to the edible shrimp stock and on the reproductive potential of the population showed that only 2.0-6.5 % of the recruits and 2.5-8.0 % of the females recruiting to the spawning stock are secondary females. The implications of these findings for the management of the shrimp fisheries are briefly reviewed.

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RESUME

Le rapport décrit les résultats des recherches histologiques sur l'inversion sexuelle chez la crevette grise, Crangon crangon (L.), et discute son effet sur le recrutement et le potentiel reproductif de la population crevettière dans les eaux côtières belges. Le pourcentage des mâles de 41-50 mm montrant des oocytes en croissance dans leurs gonades était de 2.5-3.0 % en Août et en Octobre, et de 9.2 % en Septembre. Des données sur le rapport numérique entre les sexes sont présentées et sont analysées par rapport à l'éventualité d'une inversion sexuelle. Une évaluation des effets d'une inversion sexuelle éventuelle sur le recrutement vers la phase exploitable du stock et sur le potentiel reproductif de la population a démontré que seulement 2.0-6.5 % des recrues et seulement 2.5-8.0 % des femelles s'intégrant au stock reproducteur sont des femelles secondaires. Les implications de ces résultats pour la gestion des pêcheries crevettières sont traitées.

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1. Introduction

Since BODDEKE (1961, 1962) published his hypothesis on the sex change of the brown shrimp, Crangon crangon (L.), this has been one of the most controversial aspects in the biology of this shrimp species. According to BODDEKE (1961, 1962) male brown shrimps change into females at a length of 42-46 mm and grow to an edible size as secondary females. Sex reversal would occur in March-June and in August-September, the second period being the most important one.

BODDEKE's hypothesis never has been confirmed by other investigators. MEREDITH (1952), MASON (1968), SCHOCKAERT (1968a) and LABAT (1976) could not find any evidence of sex reversal from histological studies of the gonads ; SCHOCKAERT (1968a) looked unsuccessfully for transitional stages of the secondary sexual characteristics and MEIXNER (1969) did not observe any sex change in male brown shrimps during experiments in vitro. However, most critiques on the sex change hypothesis in their turn could be criticized, e.g. because the numbers of shrimps examined were too small to be evidential or because the investigations did not cover the critical size classes or periods in which sex reversal was reported to take place.

More recently, however, TOUIR (1977) performed a comprehensive morphological and histological study on the androgenic glands of, amongst others, the brown shrimp, from which he definitely concluded that the brown shrimp is a gonochoristic species.

The present paper is an attempt to elucidate this controversy which, by now, has lasted for more than twenty years. It comprises four main parts : a histological and morphological study of the gonads, androgenic glands and external sexual characteristics, investigations on the sex-ratio of the shrimp population, an evaluation of the possible effects of sex reversal on recruitment to the edible shrimp stock and on the reproductive potential of the shrimp population and a discussion on the management implications of sex reversal.

The investigations were focused on late summer-early winter, to cover the main period during which sex reversal is supposed to take place. Moreover, if there is any effect on e.g. recruitment, this effect can be expected to be maximal in late summer and in autumn since at that time the densities of the shrimp population are growing to a peak.

2. Histological investigations

2.1. Material and methods

The shrimps used for the histological and morphological study were obtained from monthly samples taken in 1979 on different sampling stations within 10 miles off the Belgian coast. The samples were preserved in a 10 % formalin solution in sea water.

Male and female shrimps were separated according to their secondary sexual characteristics : the shape and length of the endopodite of the first pleopods (egg-bearing endopodite in females), and the presence or absence of an appendix masculina on the endopodite of the second pleopods (EHRENBAUM, 1890 in TIEWS, 1967 ; MEREDITH, 1952 ; TIEWS, 1954 and SCHOCKAERT, 1968a). At the same time the first and second pleopods were examined on the presence of transitional structures.

All the males with a length of 41-50 mm (630 specimens) from the samples of August, September and October were used for histological examination. In that way both the critical length classes and the critical months in which sex reversal could be expected (BODDEKE, 1961, 1962) were covered. Microscopic slides were obtained by the "squash method". For this purpose the gonads were dissected out, stained in an alcoholic aceto-carmine solution (LILLIE and FULLMER, 1976), and squashed between cover- and mount glasses.

2.2. Results and discussion

Sex determination by histological examination of the gonads always confirmed the results of sexing by external characteristics. Except for one spent male all the testes contained developing and mature sperm. Mostly the vasa deferentia were very distended, as they were filled with spermatozoa.

These results are in contradiction to BODDEKE (1961, 1962, 1966) who found only spent males in August and September, but they confirm the findings by SCHOCKAERT (1968a), although those were based on the examination of only 15 individuals.

In some specimens the testes contained, in addition to spermcells, also a few to numerous developing oocytes (Plate 1). They were usually found in the middle part or in the caudal ends of the testes and showed different stages of development, ranging from early ones, with a small diameter and a fairly homogeneous cytoplasm, to later ones, with a larger diameter and numerous granules.

The presence of developing oocytes in the testes is considered as an indication for a sex change from male to female (BODDEKE, 1961, 1962). However, the percentage of males showing this feature was much lower than stated by BODDEKE : 3 % in August, about 9 % in September and 2.5 % in October. The size of these males ranged from 42 to 48 mm total length, most of them measuring 45-47 mm (Table 1).

External transitional forms, with degenerating male characteristics, were not found amongst the "sex changing" males. In all cases the appendix masculina was well differentiated and the endopodite of the first pleopods was never longer than in males without developing oocytes.

These observations suggest that sex reversal in the brown shrimp would happen very quickly and without leaving any discernible external marks. Within one moult the appendix masculina would disappear completely while the endopodite of the first pleopods would grow to an egg-bearing length. Moreover, within the same critical moult the number of segments of the antennular exopodite, which is related in a sex dependent way to the number of moults (TIEWS, 1954), would not increase as usual but would decrease, and this decrease would be exactly such that immediately afterwards the secondary females cannot be distinguished from the primary ones. Such a phenomenon seems to be rather unlikely (SCHOCKAERT, 1968a and REDANT, 1972).

The absence of external transitional forms has also been described for Argis dentata, a fully protandric species of the Crangonidae (FRECHETTE, CORRIVAULT and COUTURE, 1970). In the gonad structure of this species, however, transitional stages have been reported, such as the absence of spermcells, atrophied vasa deferentia and degenerating androgenic glands, which become filled with pycnotic nuclei and cytolysosomes. Comparable stages could not be identified in the brown shrimp. The testes of the males in which developing oocytes were found always contained sperm-cells and their androgenic gland never showed a degenerating aspect.

The process of sex reversal in the brown shrimp appears to be quite exceptional as compared with the protandric species of the Pandalidae, where transitional forms can be recognized in the external sexual characteristics (shrivelling and eventually disappearing male appendages), as well as in the gonad structure (developing oocytes, degenerating vasa deferentia and androgenic glands) (BERKELEY, 1930 ; ALLEN, 1963 ; BUTLER, 1964 and CHARNIAUX-COTTON, 1960, 1970, 1975).

The androgenic gland plays an important part in the endocrine control of sex determination. In protandric species the androgenic hormone, secreted by this gland, is indispensible to maintain the external male characteristics. Sex reversal from male to female starts when the androgenic gland is degenerating and the inhibition of vitellogenesis by the androgenic hormone disappears. Later on the development of the ovary induces, by secretion of an ovarian hormone, the differentiation of the female secondary characteristics (CARLISLE and KNOWLES, 1959 ; CHARNIAUX-COTTON, 1965, 1975 ; TOUIR, 1977 and CARPENTER, 1978). However, TOUIR (1977) showed that in the brown shrimp the androgenic hormone is not required for the maintenance of the external male characteristics and therefore he concluded that the brown shrimp is a gonochoristic species.

The development and activity of the androgenic gland in their turn are controled by a neurosecretory complex, the X-organ-sinus gland, located in the eyestalks. This complex secretes an ovary-inhibiting hormone which is also involved in the regulation of sex change. The hormonal activity of this complex depends on external conditions (CARLISLE and KNOWLES, 1959 ; CHARNIAUX-COTTON, 1970, 1975 and CARPENTER, 1978).

The rôle of the environment in influencing the hormonal control of protandry, and more precisely of the maintenance or loss of the androgenic gland, is still uncertain. Recently a nutritional effect has been found in crabs. In male crabs kept under conditions of malnutrition, developing oocytes appear, but the males do not change into reproductive females (CONAN, pers. comm.). Non-functional hermaphroditism has also been shown in Talitridae (CHARNIAUX-COTTON, 1975) and in Pontastacus leptodactylus (PAYEN, 1974 in CHARNIAUX-COTTON, 1975).

Taking into account the present observations on the aspect of the androgenic gland in "sex changing" brown shrimps, it cannot be excluded that also this species is an example of non-functional protandric hermaphroditism.

3. Investigations on the sex-ratio

3.1. Material and methods

Data on the sex-ratio of the shrimp population were obtained from samples collected in July-December 1979. These samples were taken with a small meshed trawl (20 mm mesh size in the cod-end) during monthly surveys on 11 fixed sampling stations in two areas, one inshore, the other offshore, near the Belgian coast (Figure 1).

From each sample on average 250 shrimps were measured and sexed. Total lengths were measured from the tip of the scaphocerite to the distal margin of the uropods. Sexes were distinguished according to the criteria described in par. 2.1. These allowed the separation of male and female shrimps down to a length of at least 30 mm. Below this length an increasing number of shrimps could not be sexed with certainty.

For each sampling date and station the original numbers of males and females were corrected for the retention efficiency of the trawl (REDANT, 1978 and TETARD, 1985), and grouped into 5 mm length classes. Sex-ratios were calculated as the percentage of males versus the total number of shrimps in each size class.

3.2. Results and discussion

The percentages of males per size class are given in Figure 2 (by sampling date and station) and Figure 3 (monhtly averages by area). The values for the $\leqslant$ 30 mm size class, however, should be considered with caution. In some samples only part of the shrimps $\leqslant$ 30 mm could be sexed with certainty and it is doubtful whether sex-ratios calculated from such partial data give a reliable approximation of the actual sex-ratio of the $\leqslant$ 30 mm size class as a whole.

Although the sex-ratios often varied considerably from one sampling station to another, the general aspect of the relationship between sex-ratio and length was similar in all months (Figure 2). The percentage of males gradually decreased with increasing size and usually dropped to zero in the 56-60 mm (July-September) or 61-65 mm size class (October-December).

This roughly confirms earlier findings by TIEWS (1954) on the sex-ratios of undersized and edible shrimps in the German Waddensea and is in agreement with the observation by several authors (HAVINGA, 1930 ; LAFUSTE, 1953 ; MEYER-WAARDEN and TIEWS, 1957 in TIEWS, 1967 and MASON, 1968) that the stock of edible shrimps above 55 mm in length is almost exclusively composed of females.

In October-December the percentages of males per size class were about 10-30 % higher than in July-September, except for the smallest and greatest size classes (Figure 3). Most likely this was a consequence of the autumn migration of the brown shrimp, of which onset, participation and range are known to depend on sex, age and physiological condition (HAVINGA, 1930 and BODDEKE, 1975, 1976).

The average percentage of males in the population (all size classes pooled, including the ≤ 30 mm size class, and all sampling stations pooled by area) ranged from 40 to 55 %, except in October when the percentage of males in the offshore population was as low as 35 %, due to the relatively high densities of shrimps > 55 mm amongst which almost no males were found. Accordingly the overall male/female-ratio of the shrimp population in the Belgian coastal waters was estimated to be only slightly smaller than 1 (namely 0.86).

It is very difficult to compare these results with figures from the literature. Usually male/female-ratios are calculated simply by pooling the numbers of males and females over a wide range of size classes, leaving out of account that the original data are affected in a size dependent way by the selectivity of the sampling gear. Therefore the figures found in the literature are merely the male/female-ratios of catch samples and not of actual populations.

Different hypotheses have been raised to explain the almost complete absence of males in the edible shrimp catches, such as higher mortality rates of the males (MEREDITH, 1952) or the widespread occurrence of a sex change from male to female (BODDEKE, 1962).

The explanation seems to be much more evident. The average growth rate of undersized males is considerably lower than the average growth rate of females (TIEWS, 1954 ; SCHOCKAERT, 1968b and LABAT, 1977). It takes males 2-2.5 times longer than females to grow from 35 to 55 mm in length. Consequently cumulated mortalities due to e.g. predation can be expected to be higher for males than for females, even if their instantaneous mortality rates are equal. For this reason it is quite logical that the proportion of males growing to an edible size is much smaller than the proportion of females, and also that the percentage of males decreases with increasing size. The sex change hypothesis as such is not essential to explain this phenomenon. However, it is obvious that sex reversal may accelerate the decline of the sex-ratio, especially in the size classes where sex reversal is supposed to take place.

These views also imply that the percentage of males in the 31-35 mm size class can be considered as a reliable estimate of the sex-ratio at birth. Indeed, up to a length of about 35 mm male and female shrimps have similar life histories, with equal growth rates and, most probably, also equal mortality rates. In most samples from July-December 1979 this percentage ranged from 40 to

65 % (Figure 2), with an overall average of 56 % (all sampling stations and dates pooled), effectively meaning that the male/female-ratio at birth was somewhat higher than 1 (namely 1.26).

The present data do not support the hypothesis that the brown shrimp is fully protandric. In protandric species, such as *Argis dentata*, *Pandalus borealis*, *P. hypsinotus*, *P. jordani*, *P. platyceros*, *Pandalopsis dispar* and *Paratya curvirostris*, the male/female-ratio changes drastically with the onset of sex reversal. Males are clearly in the majority in the size or age classes below the critical size or age at which sex reversal occurs (male/female-ratio $\gg 1$) and are almost or completely lacking in the size or age classes above (male/female-ratio $\ll 1$) (see e.g. ALLEN, 1959 ; BUTLER, 1964 ; FRECHETTE, CORRIVAULT and COUTURE, 1970 ; CARPENTER, 1978 and JONSSON and HALLGRIMSON, 1981).

Obviously this is not the case in the brown shrimp. At birth the male/female-ratio is hardly higher than 1 and the decline in the percentage of males is not confined to the size classes in which sex reversal is supposed to take place. This suggests that, if the brown shrimp is protandric at all, only a minority of the males would change into females. This is completely in line with the results of the histological investigations.

4. Effect of sex change on recruitment and reproductive potential

4.1. Material and methods

Even though only a minority of the males would change into females it cannot be excluded that sex reversal has a considerable impact on recruitment and reproductive potential of the shrimp population. An attempt has been made to quantify these effects, starting from the basic assumption that sex reversal in the brown shrimp always is functional.

The fact that external transitional stages never have been observed in the brown shrimp suggests that primary and secondary females look perfectly alike and that it is impossible to distinguish between the two types of females. Therefore the proportion of secondary females in e.g. the edible shrimp stock cannot be established by direct observations. Instead it has to be estimated by an indirect method.

This was done by predicting the total numbers of shrimps which may have recruited to the edible shrimp stock within a limited period of time (potential recruitment), and the relative part of secondary females therein. Basically the same approach was used to estimate the share of secondary females in the potential recruitment of female shrimps to the female spawning stock, the latter being considered as an index of the reproductive potential of the population.

The estimates of potential recruitment to the edible shrimp stock and to the female spawning stock were made under the following assumptions :

(a) growth of males and females progresses along the growth curves described by TIEWS (1954) ;

(b) the mortality rates of males, primary and secondary females of the same size are identical ;

(c) sex reversal is always functional, and all secondary females will mature and reproduce in the like manner as primary females ;

(d) males having changed into females undergo a growth acceleration, similar to the one described for protandric Pandalidae (BERKELEY, 1930), and the resulting growth pattern is identical to the one of primary females of the same size.

The length frequencies of males and females mentionned under par. 3.1. served as a data-base for the calculations. These data were corrected for the retention efficiency of the trawl and averaged per month and per area. The resulting length distributions were assumed to give a reliable picture of the length and sex composition of the shrimp population.

The estimates of potential recruitment to the edible shrimp stock (i.e. the total number of shrimps which were expected to grow to a size above 50 mm in length within the next month) and the relative part of secondary females therein, were computed from :

(a) the total number of males and females recruiting to the edible shrimp stock (respectively R_{males} and $R_{females}$) ;

(b) the number of males recruiting to the edible shrimp stock as secondary females, i.e. males which were expected to change into secondary females and to grow to an edible size within the next month (R'_{males}) ;

(c) the number of already secondary females recruiting to the edible shrimp stock, i.e. males which already changed into females in the previous month, which had not yet grown to an edible size in that month, but which were expected to do so within the next month ($R'_{females}$).

The numbers of males changing into secondary females and recruiting to the edible shrimp stock within one or two months (respectively R'_{males} and $R'_{females}$) were calculated from the estimated densities of the critical size classes in which sex reversal was assumed to occur, and the corresponding percentages of "sex changers" in Table 1. Sex reversal was assumed not to have taken place in July, November and December. However, if it did it is very unlikely that the percentage of males involved would have been higher than in August or October. Preliminary computations revealed that the error introduced by this assumption was very small anyway (less than 5 % of the output).

The proportion of secondary females in the potential recruitment to the edible shrimp stock then is given by $(R'_{males} + R'_{females})/(R_{males} + R_{females})$.

Separate estimates were made for each month. Afterwards the results were integrated over the whole period (July-December) to give an overall estimate of the effect of sex reversal on recruitment.

As already stated the estimates of potential recruitment to the female spawning stock (i.e. the total number of females which were expected to grow to a "spawning" length within the next month) and the relative part of secondary females therein, were calculated along the same principles.

The lower size limit of the female spawning stock was set at 50 mm. Bibliographic data on the size range and percentage of ovigerous females (HAVINGA, 1930 ; LELOUP, 1952 and TIEWS, 1954), and direct observations on the number of egg-bearing females per size class in the samples from the Belgian coast indeed suggested that most if not all females above 50 mm in length take part in the spawning process.

4.2. Results and discussion

The estimates revealed that only 2.0-6.5 % (according to the area) of the shrimps recruiting to the edible shrimp stock during autumn and winter 1979, and only 2.5-8.0 % of the females recruiting to the female spawning stock were secondary females. Both values peaked in September-October, due to the fact that both the densities of undersized shrimps and the proportion of males changing into females showed a maximum in this period.

Although it is difficult to extrapolate these estimates over a longer period of time or over a wider geographical area it seems very unlikely that the overall effect of sex reversal on recruitment to the edible shrimp stock and on the reproductive potential of the population would have been greater than estimated. The more so since most of the assumptions on which the method relied tended to maximize the estimates. It should also be stressed that the choice of the growth rates as such does not affect the estimates, as long as the relative difference between the growth rates of males and females remains unchanged.

The results of this exercise contradict BODDEKE (1961, 1962, 1979), who claimed that sex reversal plays an "essential" part in recruitment to the edible stock and in the reproductive potential of the brown shrimp. Even under the assumption that sex reversal in the brown shrimp always is functional, its effect on recruitment and reproductive potential appears to be very small.

5. Management implications

Historically the hypothesis on the sex change of the brown shrimp and the protection of the undersized shrimps are closely linked. The argument that male shrimps would grow to an edible size as secondary females was a keystone in the pleadings to save the so-called "foddershrimps" (BODDEKE, 1962), which, at that time, were landed in great quantities by the Dutch and German shrimp fleets (ICES, 1979). The campaign which followed finally resulted in a widescale introduction of the rotating shrimp sorting machine (BODDEKE, 1971, 1973) on Dutch, Belgian and Danish shrimp vessels, and in the termination of the Dutch foddershrimp fishery in 1971 (ICES, 1979).

Yet it should be clear that there is no connection at all between sex reversal and the possible necessity to protect the undersized shrimp stock. Irrespective of the fact whether the brown shrimp is protandric or not, it might be useful to protect the undersized shrimps since part of them would anyhow have recruited to the edible stock if they had not been removed by the foddershrimp fishery. This is true for both the undersized males and females in the case of protandry, but it is equally true for the undersized females in the case of gonochorism. Moreover, in both cases the effect of protective measures on the edible shrimp catches can be expected to be fairly similar.

The crucial point in the discussion on the possible benefits of protective measures for the foddershrimps therefore is not on gonochorism or protandry, but on the survival rate of the undersized shrimps. If natural mortalities amongst these small shrimps would have been low the possible benefits from protective measures could have been considerable. However, TIEWS (1965, 1978) and REDANT (1980) showed that natural mortality caused by predation largely exceeds fishing induced mortality.

6. Conclusions

Although the occurrence of developing oocytes in the testes of male shrimps could be confirmed there is still no evidence that the brown shrimp is a fully protandric species. The observations especially on the aspect of the androgenic gland even suggest that hermaphroditism in the brown shrimp would be non-functional, which, as far as the population structure is concerned, comes to the same as if it was a gonochoristic species. The results of the investigations on the sex-ratio of the shrimp population seem to confirm this hypothesis.

Apparently the only means to solve the question whether protandry in the brown shrimp is functional or not, is by carefully designed in vitro experiments, by which individual shrimps can be followed throughout the sex reversal process.

The results of the histological investigations also show that, even if sex reversal in the brown shrimp would be functional, the percentage of males changing into secondary females would be very small anyway. As a matter of fact the possible effect of sex reversal on recruitment to the edible shrimp stock and on the reproductive potential of the population appears to be quite small too.

Finally it should be clear that there is no causal link between sex reversal and the possible necessity to protect the undersized shrimp stock. From a management point of view the discussion on sex reversal in the brown shrimp seems to be purely academical.

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Table 1 - Length frequencies of male shrimp, Crangon crangon, examined during the histological investigations and of the individuals with developing oocytes in the testes.

Total length (mm)	August		September		October	
	Number examined	With oocytes	Number examined	With oocytes	Number examined	With oocytes
41	22	-	17	-	1	-
42	19	1	41	-	3	-
43	14	-	47	-	15	-
44	7	-	37	3	29	1
45	8	-	50	12	30	-
46	13	1	39	7	36	1
47	6	1	51	8	21	1
48	8	-	39	4	19	1
49	2	-	29	-	6	-
50	-	-	19	-	2	-
Total	99	3	369	34	162	4
%		3.0		9.2		2.5

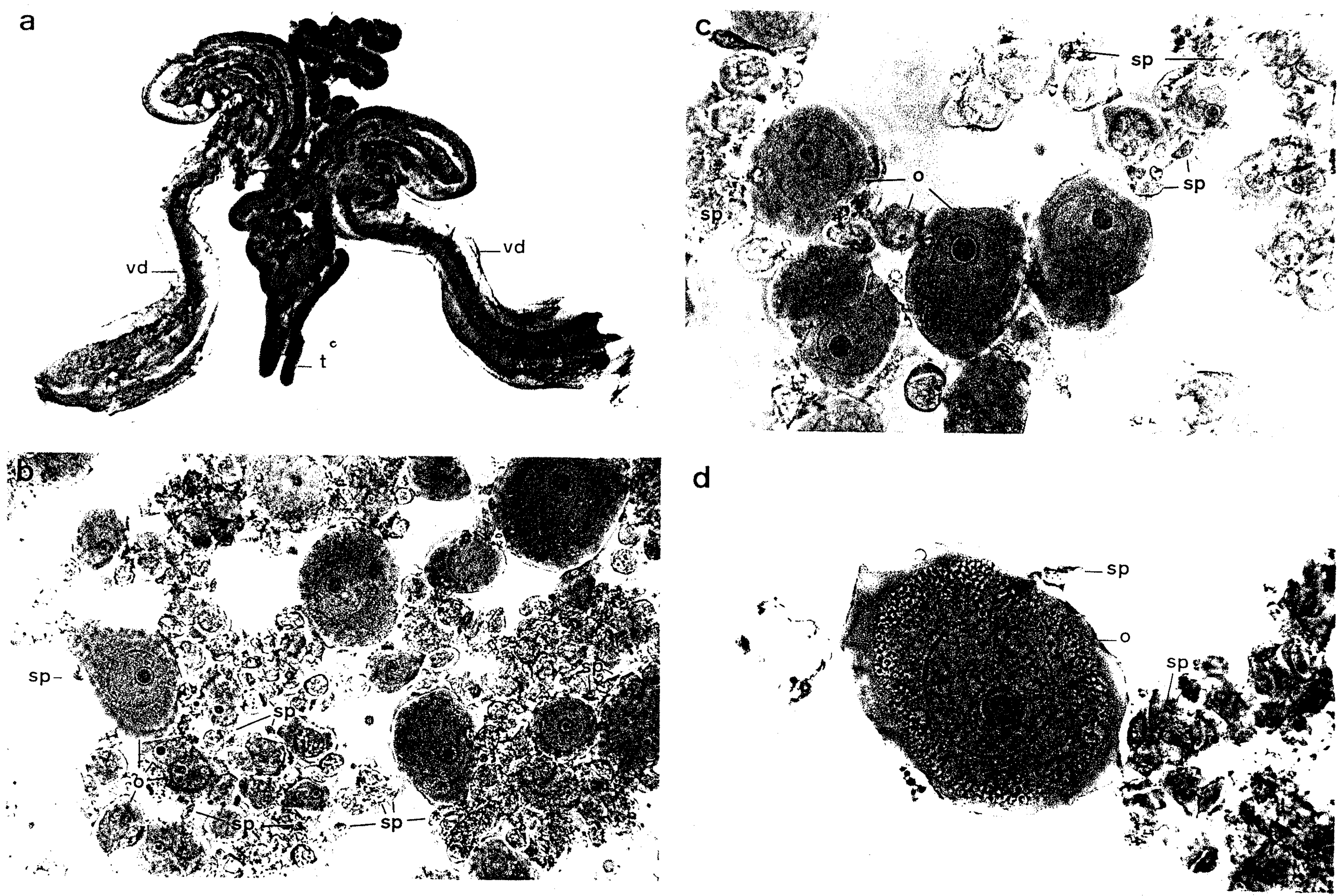

PLATE 1

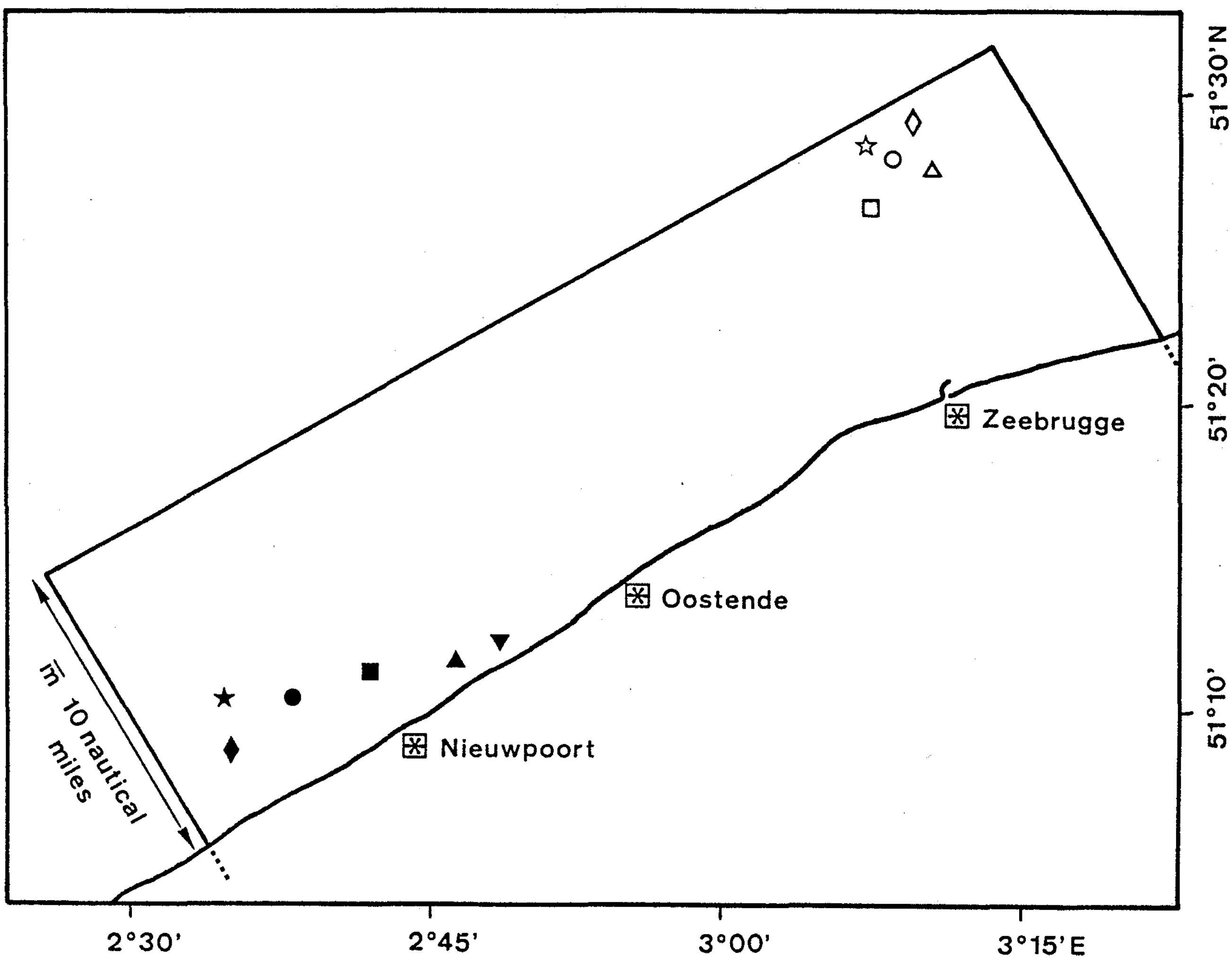

Figure 1 - Positions of the sampling stations in the Belgian coastal waters.

Open symbols : offshore sampling stations.
Filled symbols : inshore sampling stations.

Legend to Plate 1 - Microscopic slides of the gonads of male brown shrimps, Crangon crangon.

a - Testes and vasa deferentia before squashing. The vasa deferentia are filled with spermatozoa.

b/c/d - View of squashed testes tissue, showing spermatozoa and developing oocytes.

o : oocyte
sp : spermatozoa
t : testes
vd : vas deferens

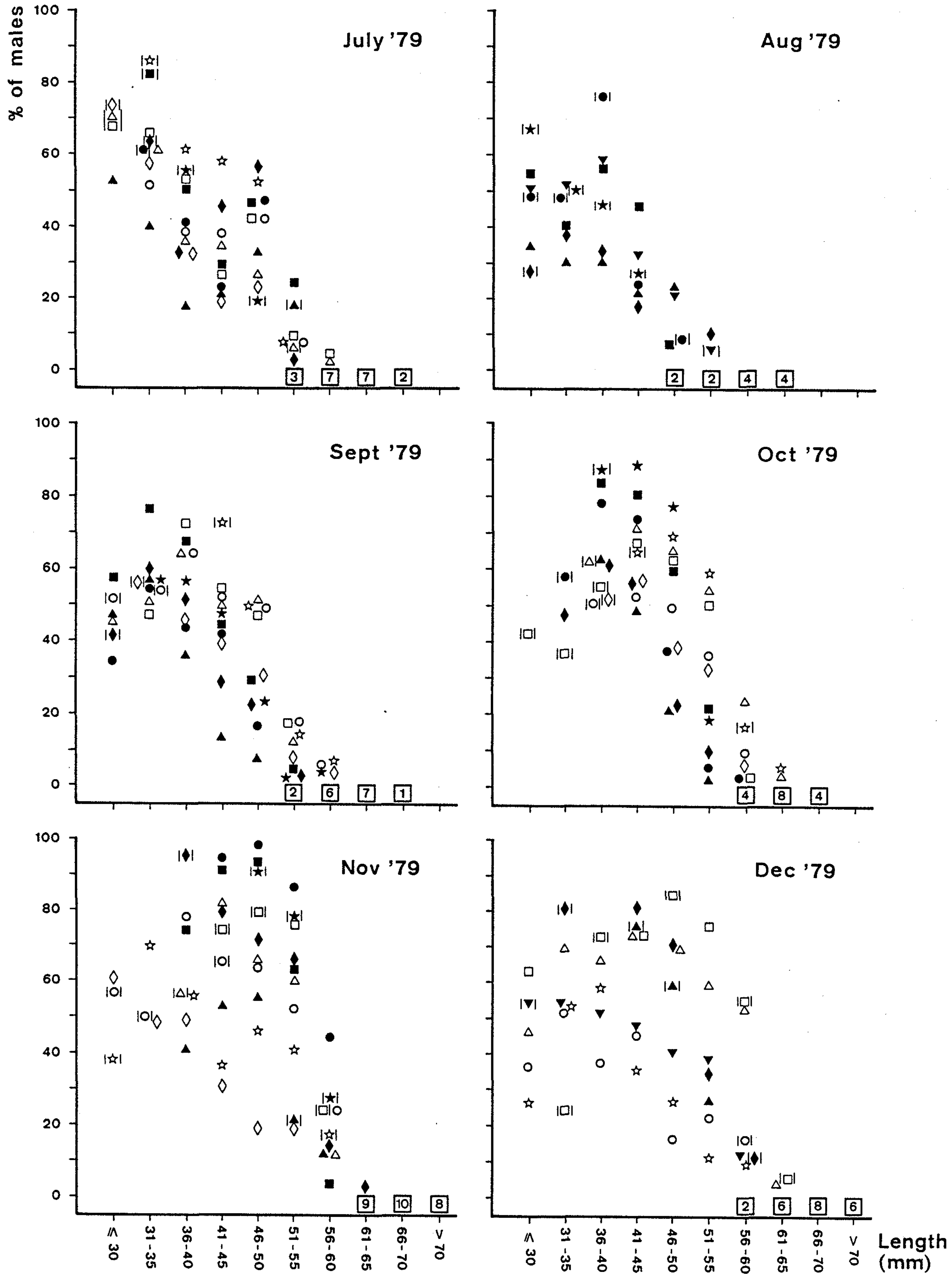

Figure 2 - Percentages of male brown shrimps, Crangon crangon, in relation to length, by sampling date and station (the symbols correspond to the ones in Figure 1).

☒ : number of observations where % of males equals zero.

|x| : observations based on only 10-20 measurements.

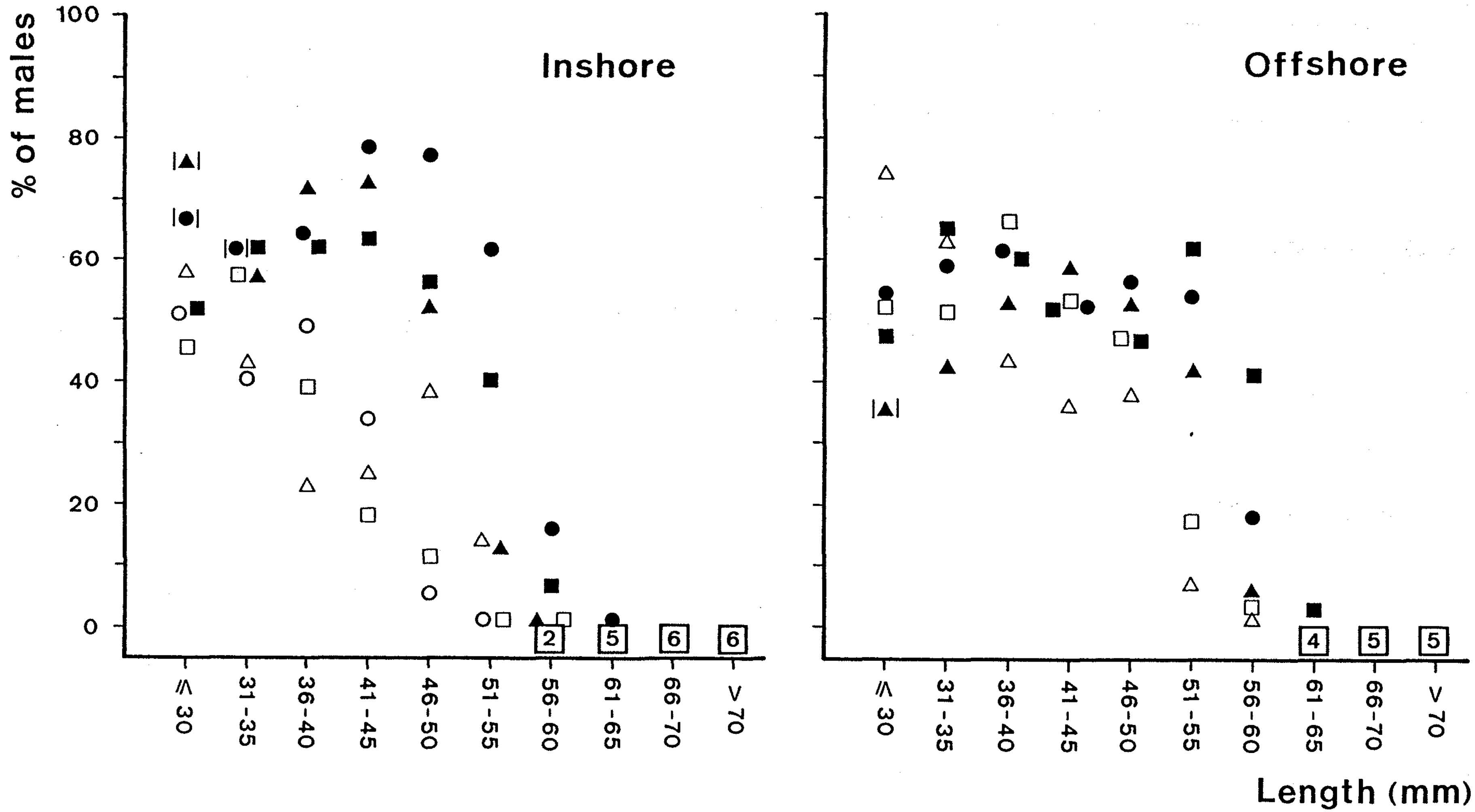

Figure 3 - Average percentages of male brown shrimps, _Crangon crangon_, in relation to length, by month and by area.

△ : July 1979
○ : August 1979
□ : September 1979
▲ : October 1979
● : November 1979
■ : December 1979
[x] : number of observations where % of males equals zero.
|x| : observations based on only 10-20 measurements.