# Estimation of Annual Growth in the Edible Crab *(Cancer pagurus* L.*)*

By

**D. A. Hancock** and **E. Edwards**
Fisheries Laboratory, Burnham-on-Crouch, Essex

Determination of annual growth under natural conditions has so far proved difficult in Crustacea, largely due to lack of information on moult frequency. In this paper, recaptures from suture-tagging experiments have been examined, and the results from crabs recaptured on annual anniversaries after their release, including both moulted and unmoulted, combined to provide estimates of annual growth and annual moult frequency. Males and females were considered separately, and annual growth in males became reduced at a smaller size than in females.

## Introduction

Yield assessments in any fishery require a knowledge of the growth rate. In Crustacea, growth is not continuous, and size increases occur only immediately after moulting when the animal is in the soft-shelled condition. Annual growth in Crustacea is therefore a function of the moult increment and the frequency of moulting.

In the edible crab fisheries of Norfolk and Yorkshire the recent use of suture tags which are not lost on moulting (MISTAKIDIS, 1959; EDWARDS, 1964 and 1965) has enabled observations to be made on the increments added under natural conditions at each moult by crabs covering a wide range of carapace width; so far, however, little is known about the frequency of moulting, owing to the very great difficulty of its determination in the field. This seems to be true also of the lobster fisheries of Great Britain which have been examined by various workers including THOMAS (1958), SIMPSON (1961) and HEPPER (1965). Yield equations developed by BEVERTON and HOLT (1957) employ parameters of the VON BERTALANFFY (1938) growth equation but, according to these authors, in their yield assessments use can also be made of growth equations of other forms. It is therefore necessary to understand the pattern of growth in Crustacea, in order to know which parameters to use. In an earlier paper (HANCOCK, 1965) the method used by GULLAND (1961) was employed to assess

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the effects of changing the legal minimum size in the Norfolk crab fishery, and it is intended to apply this method also to the Yorkshire fishery. Apart from requiring a knowledge of annual growth rate in order to obtain an estimate of total mortality from size composition data (see also HEPPER (1964) for lobsters), the assessment involved an estimate of the parameter t′ which describes the time taken for a crab to grow from the existing legal minimum size to a newly chosen one. Estimation of this parameter again requires a knowledge of the expectation of annual growth by crabs over a range of carapace widths.

By clarifying these objectives it became evident that a direct estimate of annual growth might be obtained from tagging experiments, using the average increase in size of all individuals recaptured just one year after release, irrespective of whether they had moulted once, twice or not at all, instead of trying to combine separate estimates of moult increment and moult frequency. A reappraisal of recapture data from crabs from Norfolk and Yorkshire from this point of view has resulted in a promising method for obtaining estimates of both annual growth increment and moult frequency. Although additional suture-tagging experiments are being made during the 1965–6 seasons, it was thought that early presentation of the results obtained so far might perhaps be of help to other workers on crustacean fisheries, both in examining their data and in planning future tagging experiments.

## Method

Bearing in mind the need for estimates of annual growth, data were examined from four tagging experiments, two off Norfolk, in May 1959 and May 1960, and two off Yorkshire, in June 1962 and July 1963. In both these areas the main fishing season is from April to September, with maximum catches in May and June. The carapace width increments for crabs recaptured in these experiments are set out in Tables 1–8 which are placed together at the end of this paper. From these tables crabs recaptured exactly a year (and two or three years) after release could be selected. In the Norfolk experiments all recaptures made in the year of release were examined by local Fishery Officers, who returned unmoulted crabs to the sea. Only crabs not subsequently recaptured have been recorded as first-year recaptures; subsequent recaptures were recorded at the time of the last recapture. In order to increase the numbers for analysis, crabs recaptured in April to July of the year following release in Norfolk were also included, as were those recaptured from March to July in Yorkshire. This procedure seems reasonable, since information from commercial samples examined at sea showed that in females moulting did not commence in Norfolk until July 1960 and 1961, and not until August of 1963 and July of 1964 in Yorkshire, while in both areas males usually commenced moulting about a month later. With additional recaptures it should be possible to narrow the period either side of the "anniversary" month, and therefore reduce the need for assumptions to a minimum.

The results have been plotted as annual increments against carapace widths at release, at first separately for Norfolk and Yorkshire, but subsequently combining them on to one graph (Figure 1). This again seems reasonable since some of the female crabs released off Norfolk were, in fact, subsequently recaptured off Yorkshire (EDWARDS, 1964 and 1965). The estimation of annual

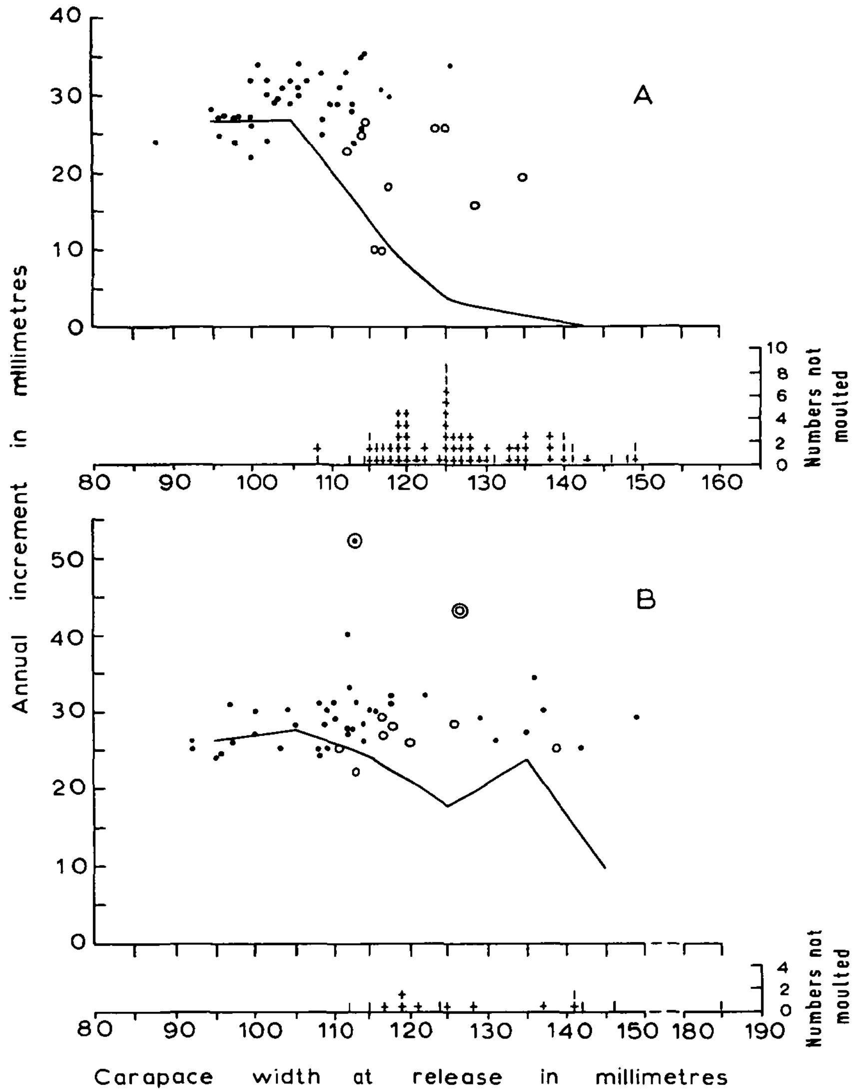


Figure 1. Graphs relating annual increments and carapace widths at release of (A) male, and (B) female, suture-tagged crabs recaptured off Norfolk (open circles) and Yorkshire (dots) (Tables 1–8). Unmoulted crabs are shown along the abscissa (+ Norfolk, | Yorkshire); circled observations, believed double moults.

growth involves averaging the values of increment at each carapace width, including both moulted and unmoulted individuals (Table 9). With the somewhat limited information available it has been necessary to group the results at 10-mm carapace width intervals, *i.e.* 110–119 mm inclusive, etc., but with more observations the same process could preferably have been applied to narrower carapace width groups, treating Norfolk and Yorkshire separately. Similarly, an estimate of moult frequency was possible within each 10-mm group, as the

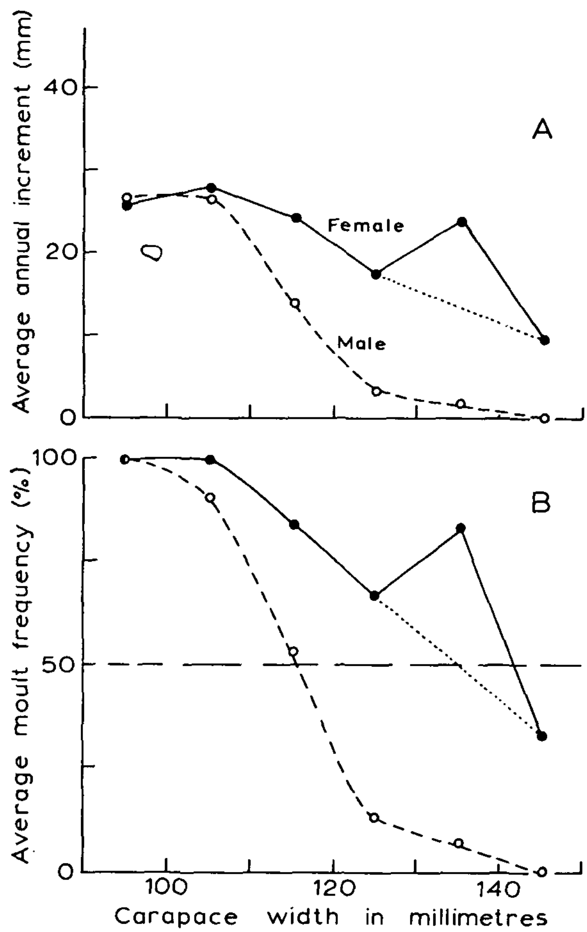


Figure 2. (A) Average annual increments taken from Figure 1 (A and B), and (B) average moult frequencies of suture-tagged crabs, calculated from the combined results of experiments off Norfolk and Yorkshire (Table 9).

proportion of all recaptures which had moulted (Table 9). From the distribution of moult increments, it is considered that only two individuals (both females, ringed in Figure 1) had moulted twice during the year before recapture. The interpretation of the actual number of moults made by any individual during this time does not affect the estimation of annual growth, which is here computed as an average increment for each range of size at release, but it does affect the estimation of average moult frequency. This has been obtained (Table 9) by dividing the total number of moults (*e.g.* in females of 110–119 mm, 19 single moults + one double moult = 21) by the number of individuals (*i.e.* 20 which moulted + 5 which did not = 25) = 21/25 or 84%.

With sufficient observations on crabs returned on the second and subsequent anniversaries of release, the same method could be applied, and the results used for comparison with the estimates obtained for the first anniversary.

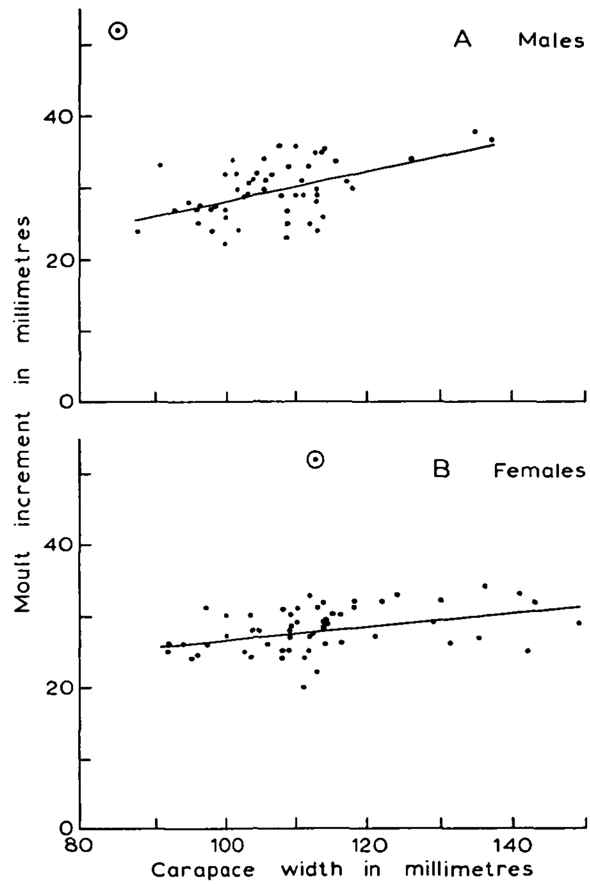


Figure 3. Fitted regression lines ($y$ on $x$) relating moult increments and carapace widths at release of suture-tagged crabs recaptured off Yorkshire (Tables 3, 4, 7 and 8); circled observations, believed double moults, excluded from regressions.
A: Regression $y = 0{\cdot}212x + 7{\cdot}008$; $r = 0{\cdot}513$ at 52 d.f.
B: Regression $y = 0{\cdot}088x + 17{\cdot}955$; $r = 0{\cdot}383$ at 56 d.f.

## Results and Discussion

Figure 2A shows, for both sexes, a convincing decline in average annual increment, steeply for males (from 26·8 mm at 105 mm carapace width to only 3·2 mm at 125 mm and none at 145 mm), and more gradually for females (from a similar increment to males at 105 mm to 17·6 mm at 125 mm and 9 mm at 145 mm carapace width). The seemingly anomalous result for females at 135 mm needs further observations before it can be decided whether it arose by chance, as the results suggest. As might be expected, the values obtained for moult frequency follow a similar pattern to annual increments (Figure 2B).

Although from Figure 2 it appears as though moulting stops altogether in males at 145 mm, it must be remembered that this result was based on only 10 individuals in that group, none of which had moulted. With more recaptures of male crabs of 140 mm and larger it is likely that some would have moulted, representing a low moult frequency which would help to account for the larger male crabs present in the catches (Figure 5). Dr. H. J. THOMAS has pointed out the possibility that selection by pots could affect the results obtained by this method, (a) if the smallest crabs in the size range tagged could escape more easily, *i.e.* for a given size at release the crabs which moulted before recapture might be retained more efficiently than unmoulted crabs, or (b) if the largest crabs found difficulty in entering the pots, *i.e.* large unmoulted crabs would be captured more efficiently than those which had moulted. These considerations, which would tend to overestimate the moult frequency of smaller crabs, and underestimate that of larger crabs, are not however thought to have affected the present results because the size range of tagged crabs in these experiments was well within the size distribution taken by pots in the commercial fishery (Figure 5), but they should be borne in mind when interpreting data of this kind.

When figures for moult frequency are sufficiently reliable a more precise estimate of annual increment might be obtained by relating moult frequency to the values of average moult increment obtained by fitting a regression line (Figure 3) to the individual moult increments recorded from recaptures throughout each season. As an example, the best estimate of moult increment for females of 120–129 mm (from Figure 3) is 29 mm, and the estimate of moult frequency for this group (Table 9: see the end of this paper) is 67%, so that the annual increment would now be calculated as $67/100 \times 29 = 19{\cdot}4$ mm (*cf* 17·6 mm obtained in Table 9).

In many species the growth rate decreases after maturity, which in the edible crab off Yorkshire seems to commence somewhere near 100 mm, the males maturing at a smaller size than females. Figure 2 also suggests that moult frequency and annual growth become reduced in both sexes above 105 mm carapace width. The males, however, show a more rapid reduction than females, and further evidence of this was found in samples collected at sea during September 1962 following the known periods of maximum moulting. The results of these samples have been expressed in Figure 4A as percentages of the numbers in each 10-mm carapace width group which had recently moulted (the shells of moulted crabs take 2–3 months to harden completely and can be easily recognized), and it can be seen that the proportion of soft-shelled individuals amongst females over 135 mm was greater than for males. It must be remembered that these graphs in fact combine the percentages of hard-shelled crabs which had not recently increased in size and soft crabs which had just reached that size as a result of moulting. It was, however, possible to use the estimate of average moult increment obtained from the regression lines in Figure 3 to replace the soft crabs at the relative carapace width from which they had most likely moulted, and this gave the new revised percentages shown in Figure 4B. This Figure resembles the general form of the moult frequency graphs in Figure 2B, though the values obtained for percentage soft crabs in the smaller size groups were less than those for moult frequency in Figure 2B. The reason for the difference between Figures 2B and 4B is not understood, but with males it might have been due in part to the fact that moulting was still in progress. In addition, it must be remembered that at their last moult hard-shelled crabs of less than 120 mm would have grown from about 90 mm or less (Figure 3). In crabs of this size, if moulting occurs more than once a

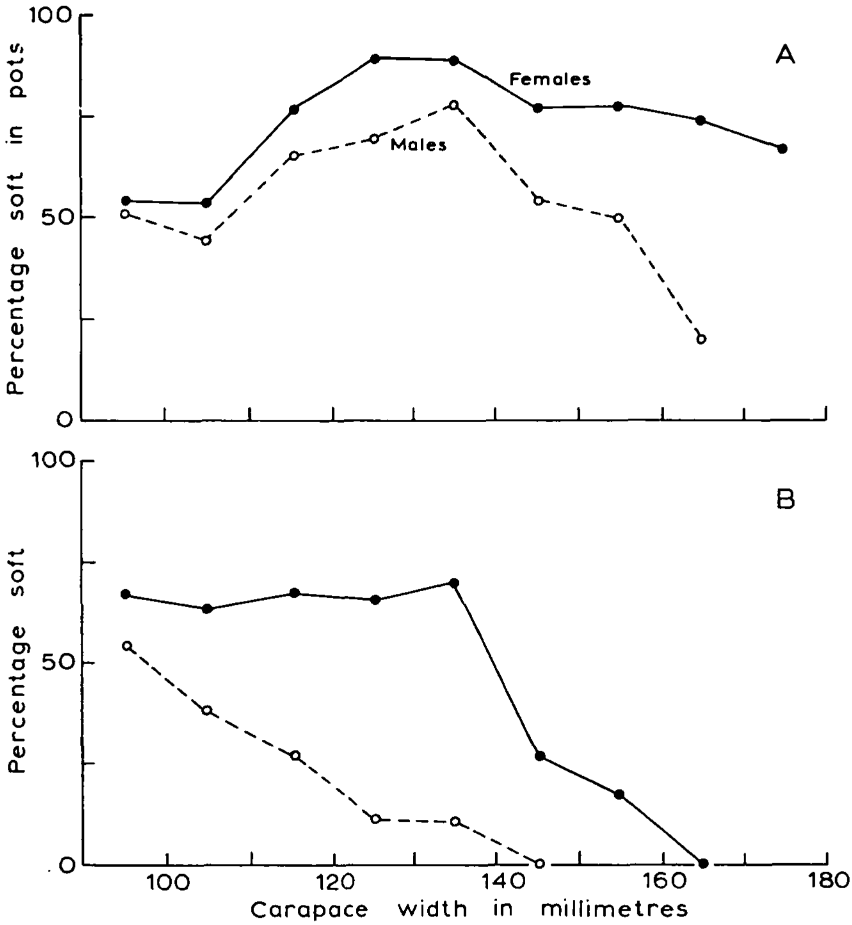


Figure 4. Soft-shelled (post-moult) crabs in samples taken in commercial pots off Yorkshire in September 1962. (A) soft-shelled crabs as percentages of the total crabs in each 10 mm carapace width group; only groups containing more than 10 observations included. (B) data of (A) replotted after soft crabs had been replaced at their pre-moult carapace widths, using information given in Figure 3.

year, the time of moulting may not coincide with that of mature crabs, *i.e.* the percentages shown in the smaller size ranges of Figure 4B may have been underestimated by combining crabs which had just moulted, with hard-shelled crabs which had moulted less than one year previously. However, examination of the percentage of soft crabs in pots is not considered to be suitable for estimating moult frequency, because of the likelihood of differing catchability between soft- and hard-shelled crabs, but it serves here to illustrate the lack of moulted large male crabs in the pots and supports the conclusions drawn from Figure 2. Examination of the size distribution of hard-shelled crabs landed in Yorkshire during 1962 (Figure 5) also confirmed that there were fewer large males than females in the commercial catches.

In the experiments described, releases were made well before moulting, so

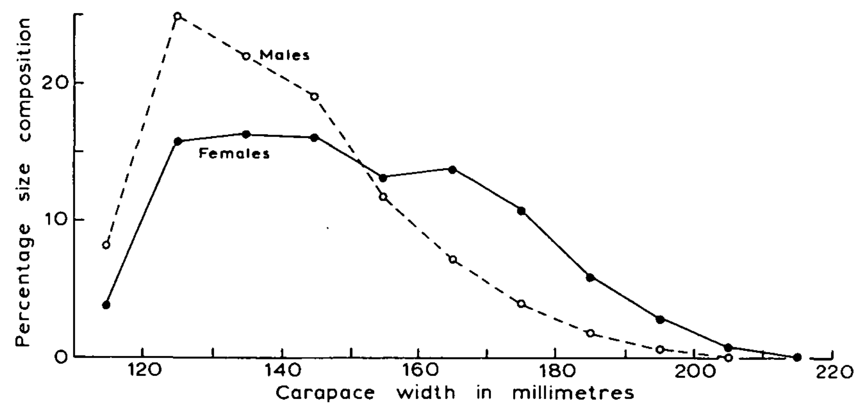


Figure 5. Average percentage carapace width distribution of 8,464 male and 9,193 female hard-shelled crabs in samples of catches landed along the Yorkshire coast throughout 1962. Observations have been grouped at 10 mm intervals, but note that the 100–119 mm group is under-represented because no crabs less than 114 mm (legal minimum size) were measured.

that all crabs recaptured near the anniversary were in the hard-shelled condition. It is important that the release and recapture periods should be clear of moulting, because it is believed that hardening crabs are hungry and might be expected to enter the pots more freely than ones which had not moulted, and this would tend to overestimate the moult frequency. It has been possible to time the liberations so as to avoid the complications of moulting, because on the east coast of England *Cancer* has a well-defined period for moulting. With lobsters, other workers suggest that this method may be difficult to apply because of the more extended moulting period. HEPPER (personal communication) has pointed out the possibility that smaller crabs, which moult more frequently, would have moulting periods separated by less than one year, and if, for example, moulting occurred every nine months, there might appear to be two moults or one per annum depending on whether tagging was done just before or just after moulting. However, in the size range of crabs liberated in these experiments the evidence suggests that the smallest were moulting no more than once per year, but this possible complication should be considered carefully when tagging smaller crabs, and may be overcome by extending the release period to two or more anniversaries. The tendency for mature females to move out of the fishery to offshore spawning grounds after moulting (MEEK, 1913) would lead to underestimation of their moult frequency. In addition, the effect of any tendency for moulted females to migrate out of the fishery to a greater or lesser extent than those which have not moulted, or for them to become less catchable when carrying eggs, should also be considered. It is not unlikely that immediately after moulting soft-shelled crabs are more subject to deaths from natural causes than are unmoulted crabs. This would lead to the underestimation of moult frequency and annual increment from tagging experiments, especially if this tendency was aggravated by the presence of the tag during moulting. However, tank observations (EDWARDS, 1965) have suggested that suture tags do not affect the survival of crabs during the moult. If, under natural conditions, moulting crabs are particularly vulnerable, tagging experiments are always likely to underestimate moult frequency.

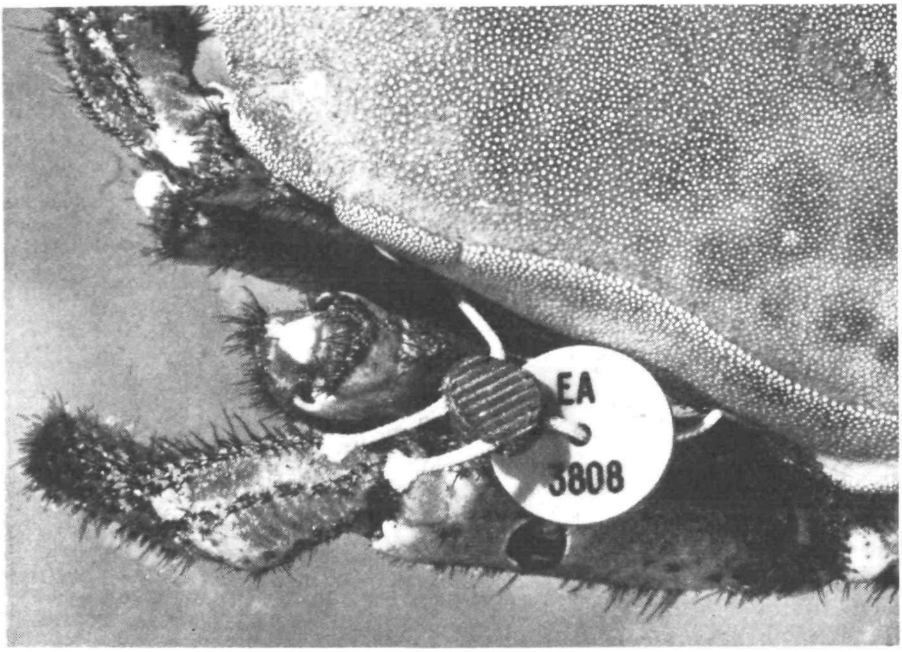


Figure 6. Suture tag attached by braided nylon through two holes pierced in the line of separation. A 6 mm lead seal clamped over the thread has been used instead of a knot to secure the tag.

## Future experiments

Examination of Tables 1–8 shows that a high proportion of the recapture data, apart from those taken near the anniversaries of date of release, were of little value when estimating moult frequency or annual growth increments. This was particularly true of recaptures obtained during the season of release, though in Norfolk arrangements were made for Fishery Officers to return to the fishery any unmoulted crabs retaken in the same year. There seems, therefore, to be a need for more experiments in which recaptures are removed from the fishery only during a short period around the anniversaries of releases. The date of release would need to be selected so as to coincide with a period of maximum fishing effort, while ensuring that recapture dates would not coincide with the onset of moulting.

In practice, this would mean that fishermen would need to be carefully briefed on the requirements of the experiment which, depending on the level of cooperation anticipated, might also include their keeping simple records of tag number, time and position of recapture of crabs returned to the fishery, perhaps also on a reward basis. The many instances of repeated recaptures of unmoulted crabs in the Norfolk fishery have already shown not only that this is practicable with interested fishermen, but also that there is a chance of increasing the proportion of recaptures taken on anniversaries. Alternatively, or perhaps in addition, the numbers of suture-tagged crabs released should be sufficient to ensure worthwhile recaptures on anniversaries of the release date, from which the most useful information is to be gained. The experimental principles described have been incorporated in a comprehensive suture-tagging experiment during 1965, when 3,400 tagged crabs were released along the east coast of England from Norfolk to Northumberland, the results of which will be presented at a later date. Crabs released in 1965 were tagged by the method described by EDWARDS (1964) except that less expensive braided terylene was used instead of nylon. In some of them the braided terylene attaching the tag was knotted, while in others a quicker method in which knots were replaced by clamped lead seals (Figure 6) was used.

## Summary

A method is described for obtaining information on annual growth increment and average moult frequency from suture-tagged crabs recaptured in the fisheries of Norfolk and Yorkshire. The method requires observations on growth increments from crabs recaptured on yearly anniversaries after release. The results showed that the moult frequency and annual growth increment become much more reduced in male crabs than in females at lengths above 100 mm, and were in agreement with the distribution of soft-shelled crabs in samples from the pots examined at sea, and with the smaller numbers of large males than females in landed catches in the Yorkshire fishery.

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For Tables 1–9 see: pages 256–64.

# Table 1

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 193 male crabs released off Norfolk, 11–15. May 1959**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1959 | | | | | 1960 | | | | | | 1961 | |
| | June | July | August | Sept. | October | April | May | June | July | August | October | June | July |
| 112 | – | – | – | – | – | – | – | 23 | – | – | – | – | – |
| 114 | NN | – | N | – | – | 26 | – | – | – | – | – | – | – |
| 115 | – | NN | NNN | – | – | – | – | NN | – | – | – | – | – |
| 116 | NN | – | – | – | – | 10 | N | – | – | – | – | – | – |
| 117 | NNN | N | NNN | – | – | 10 | – | – | N | – | – | – | – |
| 118 | N | – | NNN | N | – | – | – | – | 18, N | – | – | – | – |
| 119 | – | – | NN | N | – | – | – | – | – | – | – | – | 26 |
| 120 | N | – | – | NN | – | N | N | – | N | – | – | – | – |
| 121 | – | N | NN | – | – | – | – | – | – | – | N | – | – |
| 122 | N | N | NNN | NN | N | – | – | – | – | – | – | – | – |
| 123 | N | – | NNN | – | – | – | – | – | – | N | – | – | – |
| 125 | – | – | NNNNN | – | – | – | NNN | N | – | – | – | – | – |
| 126 | – | – | NNN | – | – | – | – | N | – | N | – | – | – |
| 127 | – | – | N | – | – | – | – | – | – | – | – | – | – |
| 129 | – | – | N | – | – | N | – | – | 16 | – | – | – | – |
| 130 | N | N | N | – | – | – | – | – | – | – | – | – | – |
| 131 | – | – | – | N | – | – | – | – | – | – | – | – | – |
| 132 | – | – | N | – | – | – | – | – | – | – | – | N | – |
| 133 | N | N | – | – | – | – | – | N | – | – | – | – | – |
| 134 | N | – | NN | – | – | N | – | – | – | – | – | – | – |
| 135 | – | N | N | – | – | 19 | N | – | – | – | – | – | – |
| 137 | – | – | – | – | – | – | – | – | – | N | – | – | – |
| 138 | – | – | N | – | – | – | – | N | – | – | – | – | – |
| 140 | N | – | – | – | – | – | – | N | – | – | – | – | – |
| 141 | – | N | – | – | – | – | – | – | – | – | – | – | – |
| 143 | – | – | N | – | – | – | – | – | – | – | – | – | – |
| 143 | – | – | N | – | – | – | – | – | – | – | – | – | – |
| 144 | – | – | – | – | N | – | – | – | – | – | – | – | – |
| 147 | NN | – | – | – | – | – | – | – | – | – | – | – | – |
| 149 | N | – | – | – | – | N | – | – | – | – | – | – | – |
| 152 | – | N | – | – | – | – | – | – | – | – | – | – | – |
| Monthly recaptures | 18 | 9 | 38 | 7 | 2 | 8 | 6 | 8 | 5 | 3 | 1 | 1 | 1 |
| Seasonal total of recaptures | | – | 74 | – | – | – | – | 31 | – | – | – | 2 | – |
| Total ewcaptures for experiment | | – | – | – | – | 107 | – | – | – | – | – | – | – |

N indicates no moult

## Table 2

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 205 male crabs released off Norfolk, 9–17. May 1960**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1960 | | | | | 1961 | | | | | | 1962 |
| | June | July | August | September | October | March | April | May | June | July | August | June |
| 114 | NN | N | NN | – | – | – | – | – | – | 25 | – | – |
| 115 | NN | – | NNN | – | – | – | – | – | – | – | – | – |
| 116 | N | NNNN | NNNNN | N | – | – | – | – | – | – | – | – |
| 117 | – | N | – | N | – | – | – | – | – | N | – | – |
| 118 | N | NN | N | – | – | – | N | – | – | – | 25 | – |
| 119 | NN | – | NNNN | NN | – | N | N | NN | N | – | NN | – |
| 120 | – | – | NNN | N | – | N | – | N | – | – | – | – |
| 121 | N | NN | – | N | – | – | – | N | – | – | 26 | – |
| 122 | N | – | NN | – | – | N | – | – | – | N | – | – |
| 123 | – | NN | N | – | N | – | – | – | – | – | – | – |
| 124 | – | – | NN | – | N | 26 | N | – | – | – | – | – |
| 125 | – | – | NN | – | – | – | N | NN | – | 26 | – | 24 |
| 126 | – | – | N | N | – | – | N | – | N | – | – | – |
| 127 | N | N | – | N | – | N | – | – | N | N | – | – |
| 128 | NN | – | N | – | – | – | NN | N | – | – | N | – |
| 129 | – | – | N | – | – | – | – | – | – | – | – | – |
| 130 | N | – | NN | N | – | – | N | N | – | – | – | – |
| 131 | – | N | N | – | – | – | – | – | – | – | – | – |
| 132 | – | N | N | N | – | – | – | – | – | – | – | – |
| 133 | – | – | – | – | – | – | – | – | N | – | – | – |
| 134 | – | – | – | – | – | – | – | N | – | – | – | – |
| 135 | – | – | – | – | – | N | – | N | – | – | – | – |
| 138 | – | – | – | – | – | N | – | – | – | N | – | – |
| 142 | – | – | N | – | – | – | – | – | – | – | – | – |
| 143 | – | – | – | – | – | N | – | – | – | – | – | – |
| 148 | N | – | – | – | N | – | – | – | – | – | – | – |
| 155 | – | – | – | N | – | – | – | – | – | – | – | – |
| Monthly recaptures | 13 | 15 | 33 | 11 | 3 | 8 | 8 | 10 | 4 | 6 | 5 | 1 |
| Seasonal total of recaptures | – | – | 75 | – | – | – | – | 41 | – | – | – | 1 |
| Total recaptures for experiment | – | – | – | – | – | 117 | – | – | – | – | – | – |

N indicates no moult

# Table 3

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 566 male crabs released off Yorkshire, 14–20. June 1962**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1962 | | | | | 1963 | | | | | | | | 1964 | | |
| | July | August | September | October | November | April | May | June | July | August | September | October | November | December | January | May | December |
| 85 | – | – | – | – | – | – | – | – | – | – | – | – | 52 | – | – | – | – |
| | – | – | – | – | – | – | – | 24 | – | – | – | – | – | – | – | – | – |
| 91 | – | – | – | – | – | – | – | – | – | 33 | – | – | – | – | – | – | – |
| 93 | – | – | 27 | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 96 | – | – | – | – | – | – | 25 | 27 | – | – | – | – | – | – | – | – | – |
| 98 | – | – | – | – | – | – | 24 | – | – | – | – | – | – | – | – | – | – |
| 100 | – | – | – | – | – | – | 27, 22 | – | – | – | – | – | – | – | – | – | – |
| 101 | – | – | – | – | – | – | 34 | – | – | – | – | – | – | – | – | – | – |
| 102 | – | – | – | – | – | – | 24 | – | – | – | – | – | – | – | – | – | – |
| 103 | – | – | – | – | – | – | – | 29 | – | – | – | – | – | – | – | – | – |
| 104 | – | – | 31 | – | – | – | – | 31 | – | – | – | – | – | – | – | – | – |
| 105 | – | – | – | – | – | – | – | – | 32, 29 | – | – | – | – | – | – | – | – |
| 106 | – | – | – | – | – | 30 | – | – | 34 | – | – | – | – | – | – | – | – |
| 108 | – | – | N | – | – | – | – | – | N | – | 36 | – | – | – | – | – | – |
| 109 | – | – | N | – | – | – | 25 | – | 27 | – | – | – | 23 | – | – | – | – |
| 110 | – | – | N | N | – | – | – | – | 29 | – | – | – | – | – | – | – | – |
| 111 | – | – | – | – | – | – | – | 29 | – | – | – | – | – | – | – | – | – |
| 112 | – | – | – | – | – | – | 33 | – | N | 25 | – | – | – | – | – | – | – |
| 113 | – | – | – | – | 30 | – | 28 | 29 | – | – | – | – | – | 35 | – | N | – |
| 114 | – | N | – | NN | – | – | – | N | – | – | – | – | – | – | – | – | – |
| 116 | N | – | 34 | – | – | – | – | N | – | – | – | – | – | – | – | – | – |
| 117 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 121 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 124 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 125 | – | – | N | – | N | – | N | – | – | – | – | – | – | – | – | – | – |
| 126 | – | – | – | – | – | – | – | 34 | – | – | – | – | – | **1** | – | – | – |
| 130 | – | – | NN | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 131 | – | N | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 133 | N | N | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 134 | – | – | – | NN | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 135 | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 136 | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 137 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 37 | – |
| 139 | – | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – |
| 144 | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 145 | – | – | – | – | – | – | – | – | – | – | – | – | N | – | – | – | – |
| 146 | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 150 | – | – | – | – | N | – | – | – | – | – | – | – | – | – | N | – | – |
| 151 | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | N |
| 156 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | N | – | – |
| 157 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 164 | – | – | – | – | – | – | – | – | – | N | – | – | – | – | – | – | – |
| 171 | – | – | – | – | – | – | – | – | – | – | – | N | – | – | – | – | – |
| Monthly recaptures | 4 | 5 | 12 | 9 | 4 | 1 | 10 | 9 | 7 | 3 | 1 | 1 | 3 | 1 | 2 | 2 | 1 |
| Seasonal total of recaptures | | | 34 | – | – | – | – | – | – | 36 | – | – | – | – | – | 5 | – |
| Total recaptures for experiment | | | | – | – | 75 | – | – | – | – | – | – | – | – | – | – | – |

N indicates no moult
Bold type observation, believed double moult

# Table 4

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 510 male crabs released off Yorkshire, 16–23. July 1963.**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1963 | | | | 1964 | | | | | | | | |
| | July | August | September | October | March | April | May | June | July | August | September | October | November |
| 92 | - | - | - | - | - | - | 28 | - | - | - | - | - | - |
| 92 | - | - | - | - | - | - | 27 | - | - | - | - | - | - |
| 98 | - | - | - | - | - | - | 27 | 27 | - | - | - | - | - |
| 100 | - | - | - | - | - | - | - | 26, 32 | - | - | - | - | - |
| 102 | - | - | - | - | 32 | - | 30 | - | - | - | - | - | - |
| 103 | - | N | - | - | - | - | - | 29 | - | - | - | - | - |
| 105 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 106 | - | - | - | - | - | - | - | 31 | - | - | - | - | - |
| 107 | - | - | - | - | - | - | 32 | - | - | - | - | - | - |
| 108 | - | - | - | - | - | - | - | - | N | 29 | - | - | - |
| 109 | - | - | - | - | - | 33 | - | - | - | - | - | - | - |
| 110 | - | - | N | - | - | - | - | - | - | - | 36 | - | - |
| 111 | - | - | - | - | - | - | - | 31 | - | - | - | - | - |
| 112 | - | - | N | - | - | - | - | - | - | - | - | - | N |
| 113 | N | N | - | N | - | - | 24 | - | - | - | - | - | - |
| 114 | N | - | N | - | - | - | 35, 26 | - | 35 | - | - | - | - |
| 115 | - | N | NN | - | - | - | - | N | - | - | - | - | - |
| 116 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 117 | - | N | - | - | - | - | - | 31 | - | - | - | - | - |
| 118 | - | - | - | - | - | - | - | - | 30 | - | 40 | - | N |
| 119 | - | - | N | - | - | - | - | - | - | - | - | - | - |
| 122 | N | - | - | - | - | - | - | - | - | - | - | - | - |
| 125 | - | - | - | - | - | - | - | N | - | - | - | - | - |
| 127 | - | - | - | - | - | - | - | - | - | - | N | - | - |
| 128 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 131 | - | - | - | - | - | - | - | - | N | - | - | - | - |
| 135 | - | - | - | - | - | - | - | - | - | - | 38 | - | - |
| 140 | N | N | - | - | - | - | - | NN | - | - | - | - | - |
| 141 | N | - | - | - | - | - | N | N | - | - | - | - | - |
| 142 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 143 | N | N | - | - | - | - | - | - | - | - | - | - | - |
| 144 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 146 | N | - | - | - | - | N | - | - | - | - | N | - | N |
| 148 | - | N | - | - | - | - | - | N | - | - | - | - | - |
| 149 | - | - | - | - | - | - | N | - | - | - | - | - | - |
| 158 | - | N | - | - | - | - | - | - | - | - | - | - | - |
| 168 | - | - | - | - | - | - | - | N | - | - | - | - | - |
| 185 | - | N | . | - | - | - | - | - | - | - | - | - | - |
| Monthly recaptures | 7 | 14 | 6 | 1 | 1 | 2 | 10 | 14 | 4 | 1 | 5 | 0 | 3 |
| Seasonal total of recaptures | - | 28 | | - | - | - | - | - | - | - | - | - | - |
| Total recaptures for experiment | - | - | - | - | 68 | - | - | - | - | - | - | - | - |

N indicates no moult

# Table 5

## Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 482 female crabs released off Norfolk, 11–15. May 1959

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1959 | | | | | | 1960 | | | | | | | 1961 | | 1964 |
| | May | June | July | August | September | November | April | May | June | July | August | September | December | May | June | May |
| 111 | – | – | – | – | – | – | 25 | – | – | – | – | – | – | – | – | – |
| 113 | – | – | – | – | – | – | 22 | – | – | – | N | – | – | – | – | – |
| 114 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 115 | – | NNNNN | – | – | – | – | – | – | – | – | 25 | – | – | – | – | – |
| 116 | – | – | N | – | – | – | – | – | – | – | 17, 21, 25 | – | – | 57 | – | – |
| 117 | – | N | – | N | – | – | – | N | – | – | – | – | – | – | – | – |
| 118 | – | NNN | NN | N | – | – | 28 | – | – | – | – | 22 | – | – | – | – |
| 119 | – | N | NN | – | – | – | – | – | N | N | – | – | – | – | – | – |
| 120 | – | NNNN | NN | N | – | – | – | 26 | – | – | – | – | – | – | 55 | – |
| 121 | – | NN | N, 30 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 123 | – | NN | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 124 | – | N | – | 25 | – | – | – | – | – | – | – | – | – | – | – | – |
| 125 | – | NNN | – | – | – | N | – | – | N | – | 21 | – | – | – | – | – |
| 126 | – | NNN | – | – | – | – | – | – | 28 | – | – | – | – | – | – | – |
| 127 | N | NNN | N | – | – | – | – | – | – | 43 | 18 | – | – | – | – | – |
| 128 | – | NNNN | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 130 | – | NN | NNN | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 131 | – | NN | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 133 | – | N | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 134 | – | NNN | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 135 | – | – | – | 20 | – | – | – | – | – | – | – | – | – | – | – | – |
| 136 | N | NNNNNN | – | – | – | – | – | – | – | – | N | – | – | – | – | – |
| 137 | – | NN | – | – | – | – | – | – | – | N | – | – | – | – | – | – |
| 138 | – | NNNNN | – | – | N | – | – | – | – | – | – | – | – | – | – | – |
| 139 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 140 | – | NN | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 141 | – | N | N | – | – | – | – | – | – | – | – | – | N | – | – | – |
| 143 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 24 |
| 147 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 152 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 153 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 156 | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Monthly recaptures | 3 | 62 | 19 | 5 | 1 | 1 | 3 | 2 | 3 | 3 | 9 | 1 | 1 | 1 | 1 | 1 |
| Seasonal total of recaptures | | – | 91 | – | – | – | – | – | – | 22 | – | – | – | 2 | | 1 |
| Total recaptures for experiment | | – | – | – | – | – | 116 | – | – | – | – | – | – | – | – | – |

N indicates no moult
Bold type observations, believed double moult

# Table 6

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 342 female crabs released off Norfolk, 9–17. May 1960**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1960 | | | | | 1961 | | | | | 1962 | 1963 | 1964 |
| | May | June | July | August | September | March | April | May | July | August | February | August | June |
| 115 | – | N | N | – | – | – | – | – | – | – | – | – | – |
| 116 | – | NNN | – | 25 | – | 29 | – | – | 27 | – | – | – | 54 |
| 117 | – | – | – | N | – | – | – | – | – | – | – | – | – |
| 118 | – | N | N | – | – | – | – | – | – | – | – | 26 | – |
| 119 | – | N | – | – | – | – | – | – | – | – | 54 | – | – |
| 120 | – | N | – | 21, N | – | – | – | N | – | 27 | – | – | – |
| 121 | – | NN | N | N | – | – | – | – | – | – | – | – | – |
| 122 | – | NN | N | – | – | – | – | – | – | – | – | – | – |
| 123 | N | N | N | – | – | – | – | – | – | – | – | – | – |
| 125 | – | – | – | 22 | – | – | – | – | – | – | – | – | – |
| 126 | – | N | NN | N | – | – | – | – | – | – | – | – | – |
| 127 | – | N | – | 23 | – | – | N | – | – | – | – | – | – |
| 128 | – | NNN | N | N | – | – | – | – | – | – | – | – | – |
| 129 | – | – | N | – | – | – | – | – | – | – | – | – | – |
| 130 | – | N | N | – | – | – | – | – | – | – | – | – | – |
| 132 | – | NNN | – | – | – | – | – | – | – | – | – | – | – |
| 133 | – | N | – | – | – | – | – | – | – | – | – | – | – |
| 134 | N | N | N | – | – | – | – | – | – | – | – | – | – |
| 135 | – | N | – | N | – | – | – | – | – | – | – | – | – |
| 138 | – | – | N | – | N | – | – | – | 25 | – | – | – | – |
| 139 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 140 | – | N | – | – | – | – | N | – | – | – | – | – | – |
| 141 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 142 | – | N | – | – | – | – | – | – | – | – | – | – | – |
| 149 | – | N | – | – | – | – | – | – | – | – | – | – | – |
| Monthly recaptures | 2 | 27 | 12 | 10 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 |
| Seasonal total of recaptures | – | – | 53 | – | – | – | – | – | 7 | – | 1 | 1 | 1 |
| Total recaptures for experiment | – | – | – | – | – | 63 | – | – | – | – | – | – | – |

N indicates no moult
Bold type observations, believed double moult

## Table 7

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 434 female crabs released off Yorkshire, 14–20. June 1962**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1962 | | | | | 1963 | | | | | | | 1964 | | | | |
| | July | August | September | October | November | April | May | June | July | August | September | October | April | May | June | September | November |
| 94 | – | – | – | – | – | – | – | – | – | 26 | – | – | – | – | — | – | – |
| 95 | – | – | – | – | – | – | – | – | 24 | – | – | – | – | – | – | – | – |
| 103 | – | – | – | – | 24 | 25 | – | – | – | – | – | – | – | – | – | – | – |
| 104 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 28 | – | – |
| 105 | – | – | – | – | – | – | 28 | – | – | – | – | – | – | – | – | 28 | – |
| 107 | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 108 | – | – | – | – | – | – | – | – | 25 | – | – | – | – | – | – | – | – |
| 109 | – | – | – | – | 27 | – | 28, 25 | – | – | – | 28 | – | – | – | – | – | – |
| 111 | – | – | – | – | – | – | – | – | – | 20 | – | 24 | – | – | – | – | – |
| 112 | – | – | – | – | – | – | N | 27 | 33, 27 | – | – | – | 25 | – | – | – | – |
| 113 | – | – | – | – | – | – | – | – | – | – | – | – | – | 22 | – | – | – |
| 114 | – | – | – | – | – | – | – | – | 28 | – | 28 | – | – | – | – | – | 32 |
| 116 | – | – | – | – | – | – | – | – | – | 26 | – | – | – | – | – | – | – |
| 119 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 121 | – | – | – | – | – | – | – | – | – | – | – | – | 27 | – | – | – | – |
| 135 | – | – | – | – | – | – | 27 | – | – | – | – | – | – | – | – | – | – |
| 141 | – | N | – | – | – | – | – | – | N | – | – | – | – | – | – | – | – |
| 142 | – | – | – | – | – | – | 25 | N | – | – | – | – | – | – | – | – | – |
| 146 | – | N | – | – | – | – | – | – | – | N | – | – | – | – | – | – | – |
| 159 | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 167 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | N | – |
| 175 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 178 | – | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 185 | – | – | – | – | – | – | – | – | N | – | – | – | – | – | – | – | – |
| 186 | – | – | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| 187 | N | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Monthly recaptures | 3 | 2 | 3 | 2 | 2 | 1 | 6 | 2 | 7 | 4 | 2 | 1 | 2 | 1 | 1 | 1 | 1 |
| Seasonal total of recaptures | – | – | 12 | – | – | – | – | – | 23 | – | – | – | – | – | 6 | – | – |
| Total recaptures for experiment | – | – | – | – | – | – | – | – | 41 | – | – | – | – | – | – | – | – |

N indicates no moult

# Table 8

**Carapace width increments (mm) related to widths at release of suture-tagged crabs. Recaptures from 490 female crabs released off Yorkshire, 16–23. July 1963**

| Carapace width at release (mm) | Month and year of recapture | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1963 | | | | | 1964 | | | | | |
| | July | August | September | October | November | February | April | May | June | July | November |
| 92 | – | – | – | – | – | – | – | 26 | 25 | – | – |
| 95 | N | – | – | – | – | – | – | 24 | – | – | – |
| 97 | – | – | – | – | – | – | 31 | 26 | – | – | – |
| 100 | – | – | – | – | – | – | 27 | – | 30 | – | – |
| 104 | – | – | – | – | – | – | 30 | – | – | – | – |
| 105 | – | N | – | – | – | – | – | – | – | – | – |
| 108 | – | N | – | – | – | – | – | – | 31 | 24 | – |
| 109 | – | – | – | – | – | – | – | 30 | – | – | – |
| 110 | – | – | – | – | – | – | – | 31 | 29 | – | – |
| 112 | – | – | – | – | – | – | 40, 27 | – | – | – | – |
| 113 | – | – | – | – | – | – | – | **52** | 31 | – | – |
| 114 | – | N | – | – | 29, 29 | – | – | – | – | 26 | – |
| 115 | – | – | – | – | – | – | – | N | 30 | – | – |
| 116 | – | – | – | – | – | – | – | – | 30 | – | – |
| 118 | – | – | – | – | – | – | 32 | 31 | – | – | N |
| 120 | – | N | – | – | – | – | – | – | – | – | – |
| 122 | – | – | – | – | – | – | – | – | 32 | – | – |
| 124 | – | – | – | – | – | – | – | – | N | – | – |
| 126 | – | N | – | – | – | – | – | – | – | – | – |
| 129 | – | – | – | – | – | – | – | – | 29 | – | – |
| 130 | – | N | – | 32 | – | – | – | – | – | – | – |
| 131 | – | – | – | – | – | – | – | – | – | 26 | – |
| 135 | – | NN | – | – | N | – | – | – | – | – | – |
| 136 | – | – | – | – | – | – | – | – | 34 | – | – |
| 137 | N | N | – | – | – | – | – | – | 30 | – | – |
| 138 | – | – | – | – | – | – | – | – | – | – | – |
| 140 | – | – | N | – | – | – | – | – | – | – | – |
| 141 | – | – | – | – | – | 33 | – | – | – | – | – |
| 146 | – | – | – | – | – | – | – | N | – | – | – |
| 147 | – | N | – | – | – | – | – | – | – | – | – |
| 149 | – | – | – | – | – | – | – | 29 | – | – | – |
| 151 | – | – | – | N | – | – | – | – | – | – | – |
| 153 | – | N | – | – | – | – | – | – | – | – | – |
| 156 | – | – | – | N | – | – | – | – | – | – | – |
| 157 | – | – | – | N | – | – | – | – | – | – | – |
| 159 | – | – | N | – | – | – | – | – | – | – | – |
| 160 | – | – | N | – | – | – | – | – | – | – | – |
| 168 | N | – | – | – | – | – | – | – | – | – | – |
| 180 | N | – | – | – | – | – | – | – | – | – | – |
| Monthly recaptures | 4 | 11 | 4 | 3 | 3 | 1 | 6 | 10 | 12 | 3 | 1 |
| Seasonal total of recaptures | – | – | 25 | – | – | – | – | 33 | – | – | – |
| Total recaptures for experiment | – | – | – | – | – | 58 | – | – | – | – | – |

N indicates no moult
Bold type observation, believed double moult

## Table 9

**Carapace width increments from crabs tagged off Norfolk and Yorkshire (Tables 1–8 and Figure 1) used to calculate average annual increment and moult frequency in 10-mm carapace width groups. Figures in parentheses, believed double moult**

| Carapace width group (mm) | Annual increments | Total increments (mm) | Moulted once | Number of individuals Moulted twice | Not moulted | Mean annual increments (mm) | Estimated moult frequency |
|---|---|---|---|---|---|---|---|
| | | MALES | | | | | |
| 90– 99 | 24, 25, 27, 27, 27, 27, 28 | 185 | 7 | 0 | 0 | $\frac{185}{7} = 26{\cdot}4$ | $\frac{7}{7} = 100\%$ |
| 100–109 | 22, 24, 25, 26, 27, 27, 29, 29, 29, 30, 30, 31, 31, 32, 32, 32, 32, 32, 33, 34, 34 | 589 | 20 | 0 | 2 | $\frac{589}{22} = 26{\cdot}8$ | $\frac{20}{22} = 91\%$ |
| 110–119 | 10, 10, 18, 23, 24, 25, 26, 26, 28, 29, 29, 29, 30, 31, 31, 33, 35, 35 | 472 | 18 | 0 | 16 | $\frac{472}{34} = 13{\cdot}9$ | $\frac{18}{34} = 53\%$ |
| 120–129 | 16, 26, 26, 34 | 102 | 4 | 0 | 28 | $\frac{102}{32} = 3{\cdot}2$ | $\frac{4}{32} = 13\%$ |
| 130–139 | 19 | 19 | 1 | 0 | 13 | $\frac{19}{14} = 1{\cdot}4$ | $\frac{1}{14} = 7\%$ |
| 140–149 | | 0 | 0 | 0 | 10 | 0 | $\frac{0}{10} = 0\%$ |
| | | FEMALES | | | | | |
| 90– 99 | 24, 24, 25, 26, 26, 31 | 156 | 6 | 0 | 0 | $\frac{156}{6} = 26{\cdot}0$ | $\frac{6}{6} = 100\%$ |
| 100–109 | 24, 25, 25, 25, 27, 28, 28, 30, 30, 30, 31 | 303 | 11 | 0 | 0 | $\frac{303}{11} = 27{\cdot}5$ | $\frac{11}{11} = 100\%$ |
| 110–119 | 22, 25, 26, 27, 27, 27, 27, 28, 28, 29, 29, 30, 30, 31, 31, 31, 32, 33, 40, (52) | 605 | 19 | 1 | 5 | $\frac{605}{25} = 24{\cdot}2$ | $\frac{21}{25} = 84\%$ |
| 120–129 | 26, 28, 29, 32, (43) | 158 | 4 | 1 | 4 | $\frac{158}{9} = 17{\cdot}6$ | $\frac{6}{9} = 67\%$ |
| 130–139 | 25, 26, 27, 30, 34 | 142 | 5 | 0 | 1 | $\frac{142}{6} = 23{\cdot}7$ | $\frac{5}{6} = 83\%$ |
| 140–149 | 25, 29 | 54 | 2 | 0 | 4 | $\frac{54}{6} = 9{\cdot}0$ | $\frac{2}{6} = 33\%$ |