THE DISTRIBUTION OF CRABS IN DALE ROADS (MILFORD HAVEN: PEMBROKESHIRE) DURING SUMMER

By J. H. CROTHERS

*Dale Fort Field Centre**

The distribution of eight common crab species in Dale Roads was investigated by baited trapping. The resultant patterns suggest the presence of a critical factor, yet to be isolated but probably related to salinity, that effectively limits most *Carcinus maenas* (L) to water of less than 3 fathoms (5·5 m.) depth and all other species to deeper water. A second critical depth zone, apparent for three of the other species, may possibly be related to a change of substrate.

Introduction

Most published accounts of crab biology are concerned with a single species (e.g. *Carcinus maenas*, Naylor, 1962) or with a single aspect (e.g. food, Muntz *et al.*, 1965) and very little has appeared about comparative distribution. This paper describes a preliminary survey of local distribution in the shallow water of Dale Roads, Milford Haven, during the summers (July to September inclusive) of 1964–1966.

It was apparent from various fauna lists that British coastal crabs can be divided into "onshore" and "offshore" species, and that for all species there exists a critical depth zone between 3 and 6 fathoms (5·5–11 metres): no species being equally abundant on both sides of the zone. It was not clear, however, whether one critical zone applied to all species, or whether there were a number of separate zones. Nor was it possible to deduce any explanation for its, or their, existence. This survey, originally designed simply to establish the seaward limit of *Carcinus maenas* as part of a larger programme on the biology of that species, has produced data showing the existence of a single critical zone for all the crab species encountered, and permitting discussion of the factors that produce it.

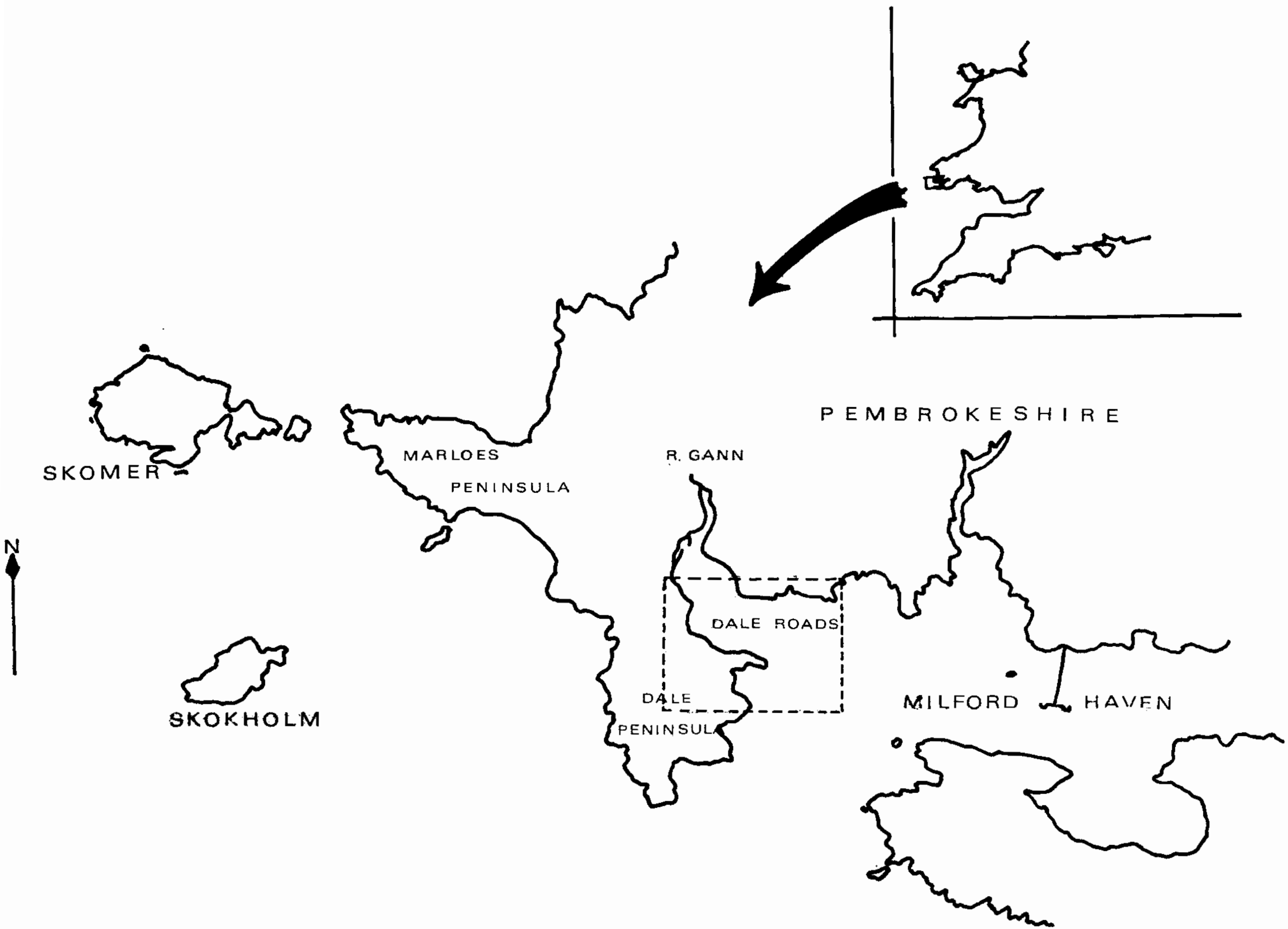
This is one of a number of papers describing distribution patterns in Milford Haven against which any changes resulting from the industrialization of the Haven (oil pollution, or increases in temperature from a new power station) can be measured.

The term "crab" is used rather loosely to include hermit crabs (Paguridea) as well as true crabs (Brachyura). Nomenclature follows the Dale Fort Marine Fauna (Crothers, 1966) except that *Eupagurus* is here called *Pagurus*.

The survey area

Milford Haven has a rich crab fauna (Crothers ,1966) and Dale Roads, a sheltered bay near the mouth (Map 1) has proved an excellent site for the study of distribution in shallow water. The bottom, an almost uniform deposit of muddy sand, slopes gently from the shores of Dale Beach and the Gann Flat (described by Bassindale and Clark, 1960) down to and below the 6 fm. line, with no rocky outcrops or other irregularities to complicate the pattern. The steep rocky shores bordering the Roads to the north and south drop quickly to the sand table, almost always within the 3 fm. line.

* Present address: The Leonard Wills Field Centre, Nettlecombe Court, Williton, Nr. Taunton, Somerset.



MAP 1.
Southwest Pembrokeshire: the area studied in detail during this survey is shown by the dotted rectangle.

METHODS

Despite its many disadvantages, trapping was chosen as the sampling method to provide the most accurate information on locality. Ten Leakey "Universal" traps (Fig. 1), fitted with ½ in. mesh courlene netting, were available during the survey and proved most successful. The ingenious method of retaining the catch within the trap cannot seriously restrict the entry of active crabs for several catches of more than 60 crabs per trap were obtained, and once 300 crabs were taken (see p. 118). However, the aperture is too small to admit adult *Cancer pagurus* or *Maia squinado*, and young crabs of all species can pass through the meshes.

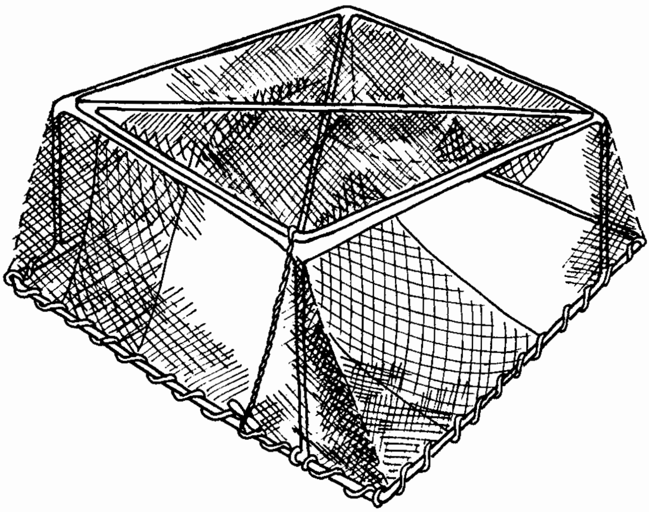


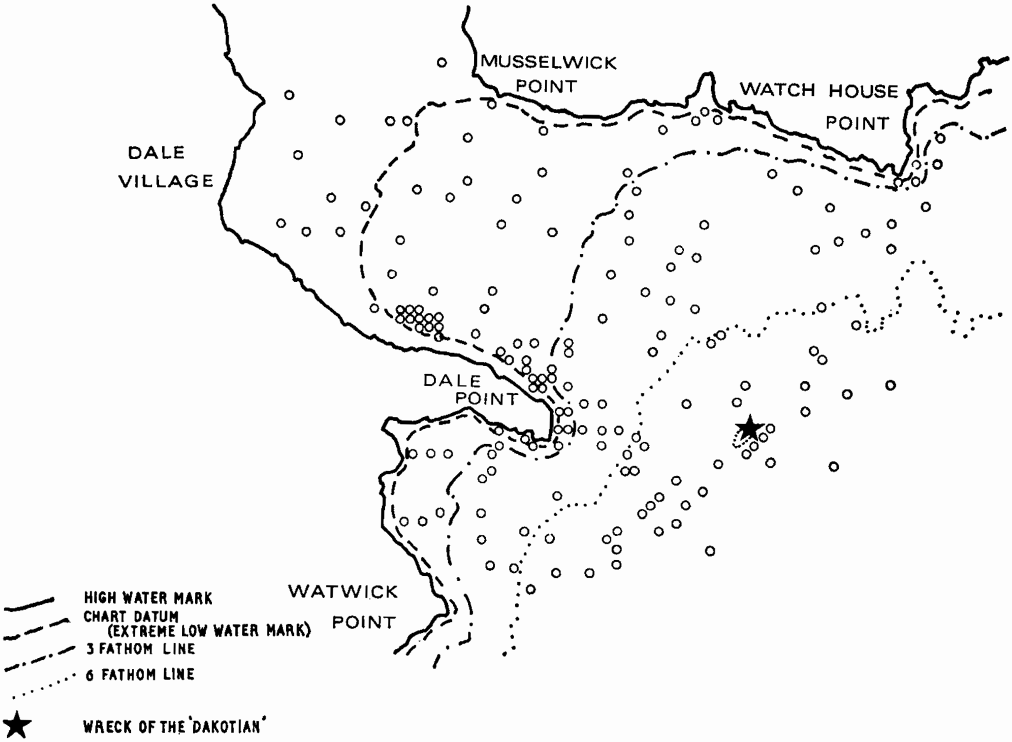
FIG. 1.
The Leakey "Universal" Trap.

The traps were baited with offal. Other baits were occasionally used in addition and no evidence was noted of any species preference for a particular bait. The baited traps were set and collected from a total of 255 positions by the author in a rowing dinghy. They were left in position for at least 24 hours and occasionally for longer periods when bad weather prevented collection. The trap positions (shown on Map 2) were established by triangulation and plotted on the Admiralty chart of Milford Haven (No. 3274, 1961). Depths were read off from the chart, rather than attempting direct measurements from a small dinghy in a choppy sea that would, in any case, require laborious correction for tidal level.

RESULTS

Thirteen species were taken in the traps:

Pagurus bernhardus L.
Anapagurus hyndmanni (Thompson).
**Ebalia tuberosa* (Pennant).
Cancer pagurus (L.).
Macropipus puber (L.).
**Macropipus arcuatus* (Leach).



Map 2.
Dale Roads showing the distribution of traps.

***Macropipus holsatus* (Fabricius).
Macropipus depurator (L.).
Carcinus maenas (L.).
**Maia squinado* (Herbst).
Inachus dorynchus (Leach).
**Inachus leptochirus* (Leach).
Macropodia rostrata (L.).

Five of these (*) were taken on less than four occasions and are not considered further: their known distribution around Dale is summarized by Crothers (1966). The numbers of individuals from the other eight species trapped at the various depths are shown in Table 1. These figures were divided by the number of traps set to provide directly comparable numbers. Then, to show up the variations in distribution, they were expressed as percentages for each species (the figures in brackets in Table 2) and plotted in Fig. 2. From this it will be seen that each of the eight species fits one of three patterns showing abundance, (1) decreasing with increasing depth of water, (2) reaching a peak between 3 and 6 fathoms, and (3) increasing with increasing depth.

Table 1. *The number of crabs trapped in Dale Roads.*

Species	Depth Range				Total
	On the Shore	0–3 fm.	3–6 fm.	below 6 fm.	
Pagurus bernhardus	4	150	175	188	517
Anapagurus hyndmanni	0	0	1	15	16
Cancer pagurus	2	7	12	3	24
Macropipus puber	2	12	16	13	43
Macropipus depurator	0	1	6	9	16
Carcinus maenas	1,740	1,061	100	4	2,905
Inachus dorynchus	0	0	8	6	14
Macropodia rostrata	0	3	10	26	39
Total	1,748	1,234	328	264	3,574

The distribution patterns

(1) *Species showing decreasing abundance with increasing depth of water*

Carcinus maenas (Map 3) alone falls into this group. Although it has occasionally been found in deeper water (e.g. Broekhuysen, 1936; Chumley, 1918), both Naylor (1962) at Swansea and the Marine Biological Association (1957) at Plymouth record 3 fm. as the usual seaward limit. During this survey *Carcinus maenas* was taken down to and below 6 fm., but 96 per cent of the 2,905 crabs trapped were within the 3 fm. line.

Table 2. *The numbers of crabs trapped divided by the number of traps set. This figure then expressed (in brackets) as a percentage for each species.*

Species	Depth Range				Total
	On the Shore	0–3 fm.	3–6 fm.	below 6 fm.	
Number of traps	71	90	47	47	
Pagurus bernhardus	0·06 (1)	1·6 (18)	3 (35)	4 (46)	8·66 (100)
Anapagurus hyndmanni	0 (0)	0 (0)	0·02 (6)	0·3 (94)	0·32 (100)
Cancer pagurus	0·03 (7)	0·08 (19)	0·25 (60)	0·06 (14)	0·42 (100)
Macropipus puber	0·03 (4)	0·13 (19)	0·34 (48)	0·20 (29)	0·70 (100)
Macropipus depurator	0 (0)	0·01 (3)	0·12 (36)	0·20 (61)	0·33 (100)
Carcinus maenas	25 (64)	12 (31)	2 (5)	0·08 (0·2)	39·08 (100·2)
Inachus dorynchus	0 (0)	0 (0)	0·17 (57)	0·13 (43)	0·30 (100)
Macropodia rostrata	0 (0)	0·03 (4)	0·21 (28)	0·50 (68)	0·74 (100)

It is by far the most numerous trappable species in Dale Roads and the only one present in the estuary of the River Gann. In summer most of the population feeds on the shore at high tide and either retires under cover or moves down the shore to below low tide mark on the ebb. Those trapped below the 3 fm. line (4 per cent of the total) probably do not feed on the shore at all and remain all the time beneath the tide marks (Crothers, 1968).

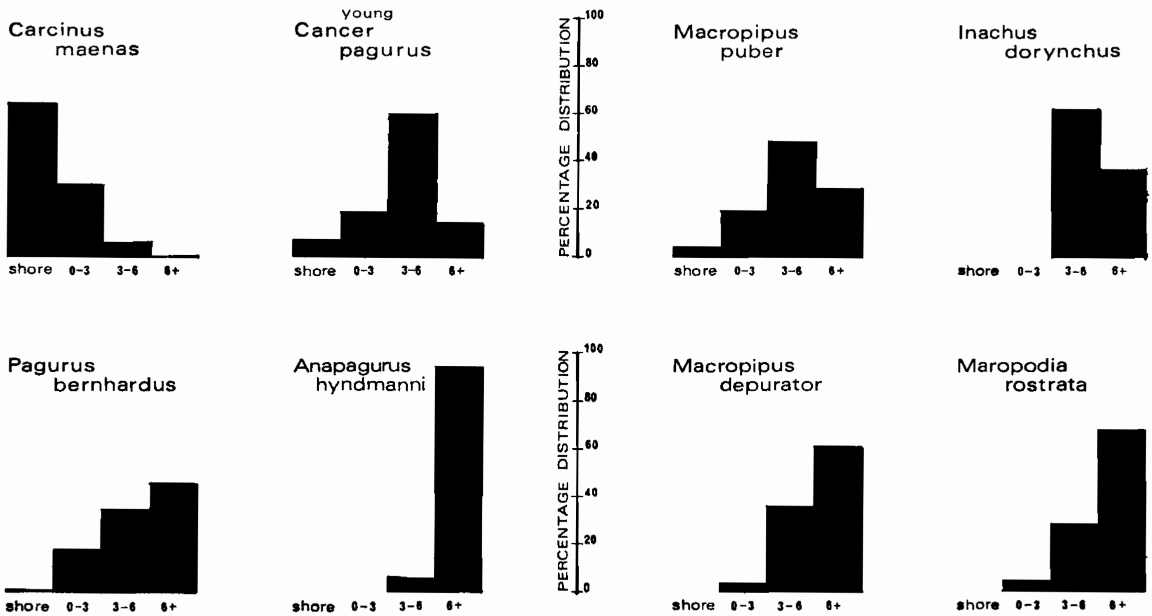
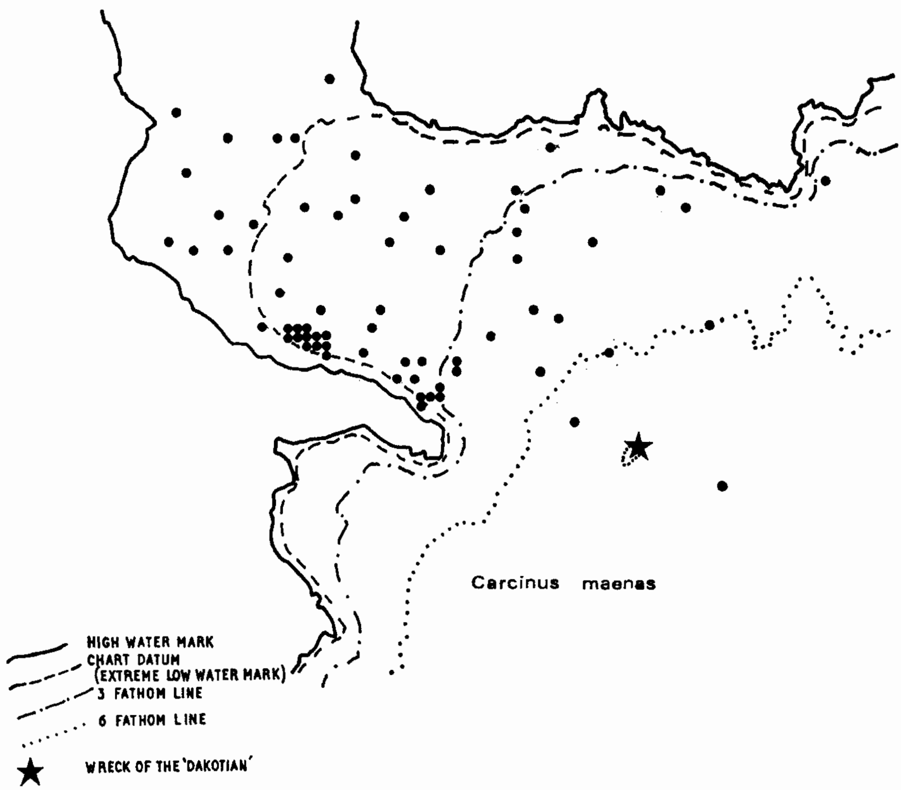


Fig. 2.
The percentage distribution with depth of the eight common crab species in Dale Roads. S, on the shore, i.e. above extreme low water of spring tides. 0–3, between extreme low water of spring tides and the 3 fm. line. 3–6, between 3 and 6 fm, 6+, deeper than 6 fm.
(data from Table 2)

(2) *Species showing abundance reaching a peak between 3 fm. and 6 fm.*
small *Cancer pagurus* (Map 4).
Macropipus puber (Map 5).
Inachus dorynchus (Map 6).

Cancer pagurus is known from depths of at least 80 fm. (146 m.) (e.g. Bruce *et al.*, 1963), but the young crabs, such as are taken in the traps used for this survey, remain in shallow water during the summer (Cole, 1956). *Macropipus puber* is a strictly coastal species (although Bouvier (1940) mentions a record from 35 fm. (70 m.)); at Plymouth the seaward limit is given as 5 fm. (9 m.) (Marine Biological Association, 1957) whilst around the Isle of Man it is rare beneath the tidemarks (Bruce *et al.*, 1963).

At Plymouth, *Inachus dorynchus* is regarded as an "inshore species" (Marine Biological Association, 1967) and near the Isle of Man, Hartnoll (1963), recorded it most often from his stations at 5 fm., 5–10 fm. (9–18 m.), and 5–15 fm. (18–27 m.).

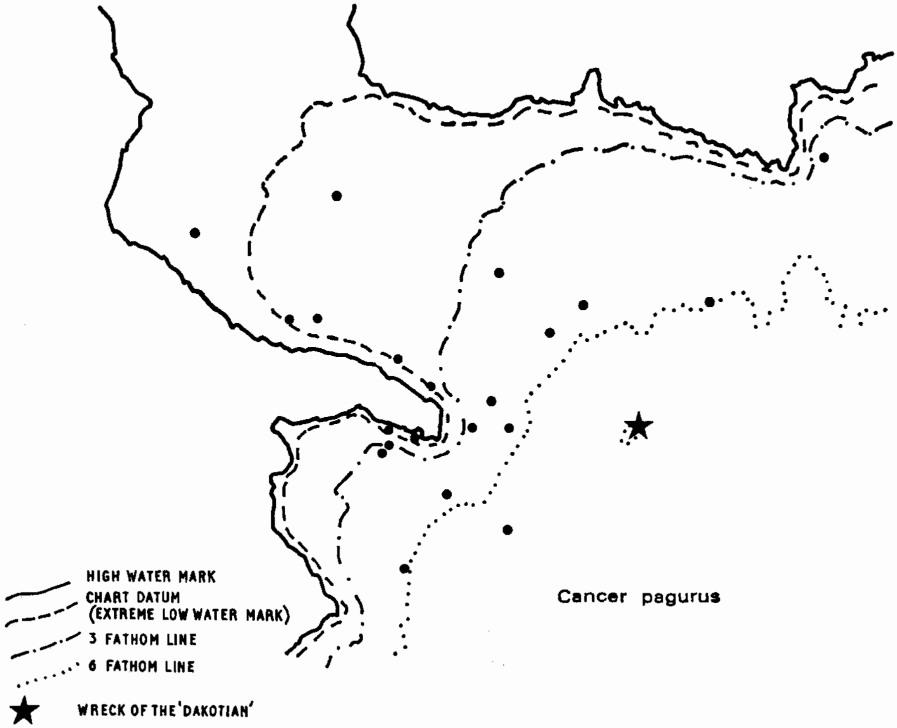


MAP 3.
Dale Roads: the distribution of *Carcinus maenas* in traps.

(3) *Species showing increasing abundance with increasing depth of water*
Pagurus bernhardus (Map 7).
Anapagurus hyndmanni (Map 8).
Macropipus depurator (Map 9).
Macropodia rostrata (Map 10).

Pagurus bernhardus, the most widespread species encountered during this survey, is the only one of the four to be found regularly on the shores around Dale Roads. Large adults, however, in *Buccinum* shells, are common only below the 3 fm. line and Selbie (1921) gives 0–15 fm. as the optimum range for this species. A few of the large crabs may migrate up the shore with the tide in the manner of *Carcinus maenas*, for one was trapped on a rocky shore in calm weather in a place where none could be found at low tide.

Selbie (1921) recorded *Anapagurus hyndmanni* as most abundant between 4 fm. (7·3 m.) and 8 fm. (14·6 m.), although extending from the shore down to about 30 fm. (55 m.). Bruce *et al.*, 1963, give 0–34 fm. (0–62 m.). At Dale a few additional specimens were obtained by dredging, but only within the depth range (and mostly



Map 4.
Dale Roads: the distribution of young *Cancer pagurus* in traps.

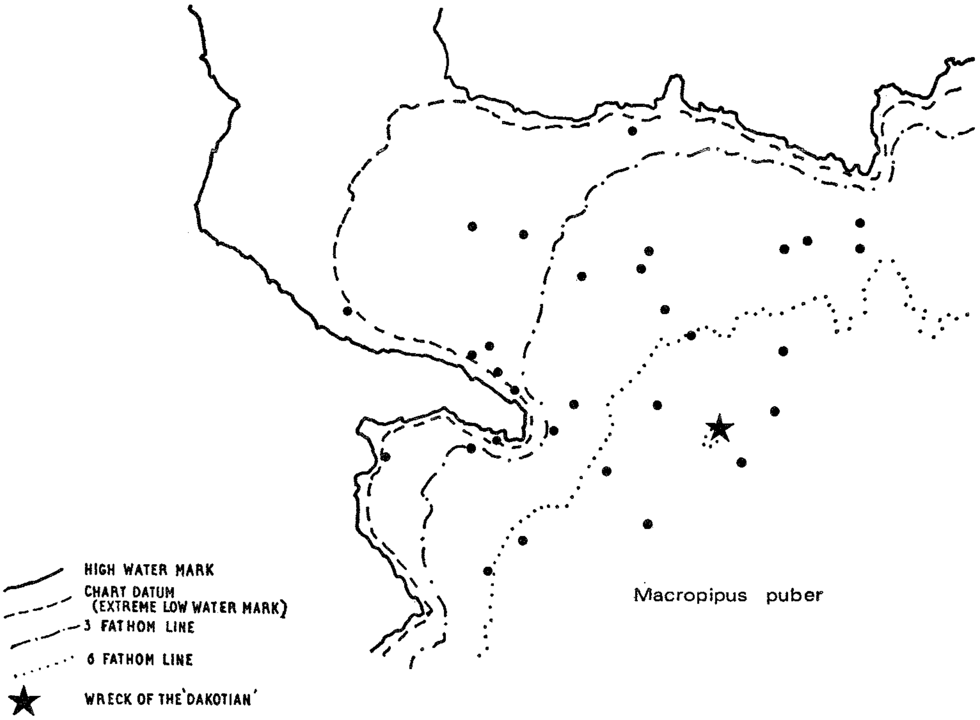
within the area) indicated by trapping. The pattern emerging from Fig. 2 suggests a preference for water deeper than 6 fm. and Miss Brigitte Loos (Crothers, 1966) found this species abundant at 15 fm. off Martin's Haven.

The vertical range of *Macropipus depurator* at Plymouth is 3–43 fm. (5·5–79 m.) (Marine Biological Association, 1957), and 3–80 fm. (5·5–146 m.) around the Isle of Man (Bruce *et al.*, 1963). At Dale a few individuals have been taken within the 3 fm. line but Map 9 is probably correct in showing this as the usual inshore limit here as well. *Macropipus depurator* appears commoner at depths below 9 fm. (16 m.) off Martin's Haven than anywhere in Dale Roads (more were collected by divers there in one day than were taken in Dale Road by diver, dredge and trap in three years).

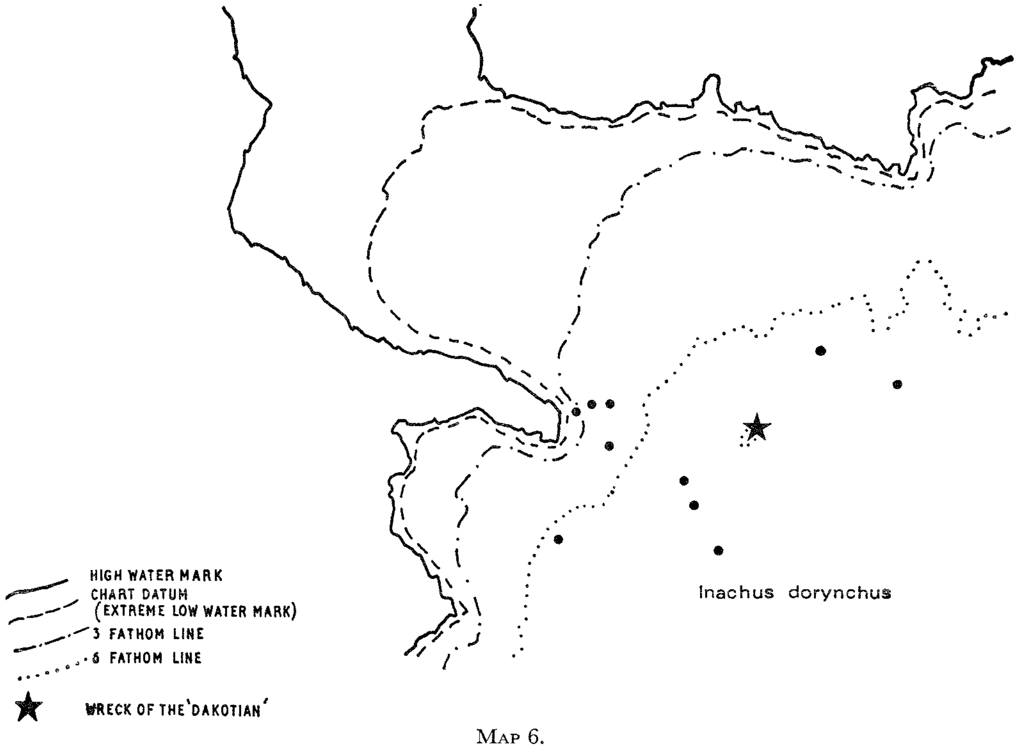
Macropodia rostrata is easily the commonest spider crab in Milford Haven, although *Maia squinado* attracts more attention in some years. Hartnoll (1963) recorded it off the Isle of Man in greatest numbers between 5 fm. and 20 fm. (9–37 m.), i.e. a little further to seaward than *Inachus dorynchus*; a pattern confirmed by Fig. 2.

Discussion

Direct comparison of the *numbers* of the various species trapped (Table 1) may be misleading on account of varying food preferences which will influence the



MAP 5.
Dale Roads: the distribution of *Macropipus puber* in traps.



MAP 6.
Dale Roads: the distribution of *Inachus dorynchus* in traps.

attractiveness of the bait. But comparisons of the *proportions* of each species trapped at various depths is valid. Discussion thus centres on the maps and Fig. 2 rather than Table 1.

The results suggest that two critical depth zones exist in Dale Roads, one, at or near 3 fm., for all species and the other, at or near 6 fm., for group 2 species only.

The 3 fm. Depth Zone

In this depth zone the distribution of *Carcinus maenas* differs from that of all other species in increasing in abundance towards the shore. Where *Carcinus* is most abundant the other species are found least often, and where it becomes relatively scarce the others increase.

Factors limiting the seaward distribution of Carcinus maenas

Two of the most obvious environmental factors that change with depth, pressure and light intensity, are unlikely to be of importance. No one has demonstrated a pressure response in adult *Carcinus maenas*, and the animal is well known to be most active under conditions of reduced light intensity, i.e. at night (e.g. Naylor, 1958). Broekhuysen (1936) showed this crab to be an estuarine rather than a marine species, and whilst it can tolerate full seawater indefinitely it prefers water of slightly reduced (below 31‰) salinity. No detailed measurements of bottom salinity have been made for Dale Roads, but the shore and shallow water must be areas of fluctuating salinity whilst bottom water below 3 fm. is presumed to remain fully saline.

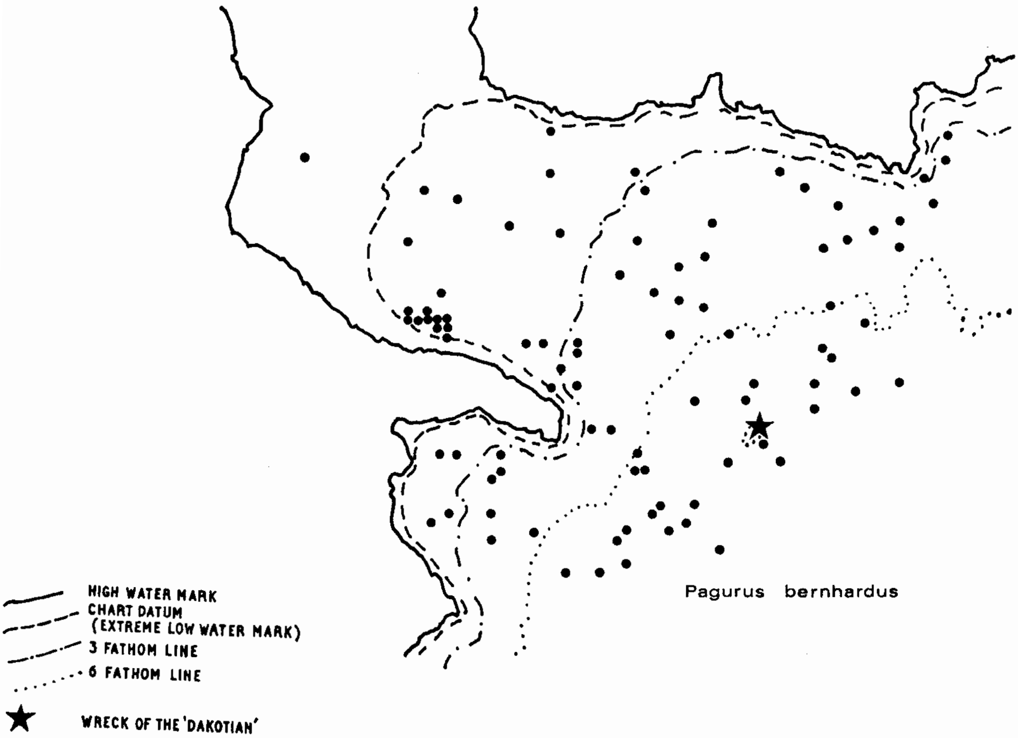
There is no evidence of any selective predation that might restrict *Carcinus* to shallow water. Indeed the only crab predators recorded as taking more *Carcinus* than other species are birds (see Crothers (1968), for references) which probably collect crabs from well within the 3 fm. line.

There is no suggestion that food preferences would limit this crab's distribution for it has been impossible to separate the potential prey of *Carcinus* from that of the other cancroid crabs encountered in this survey, on any criteria except size (see Muntz *et al.*, 1965).

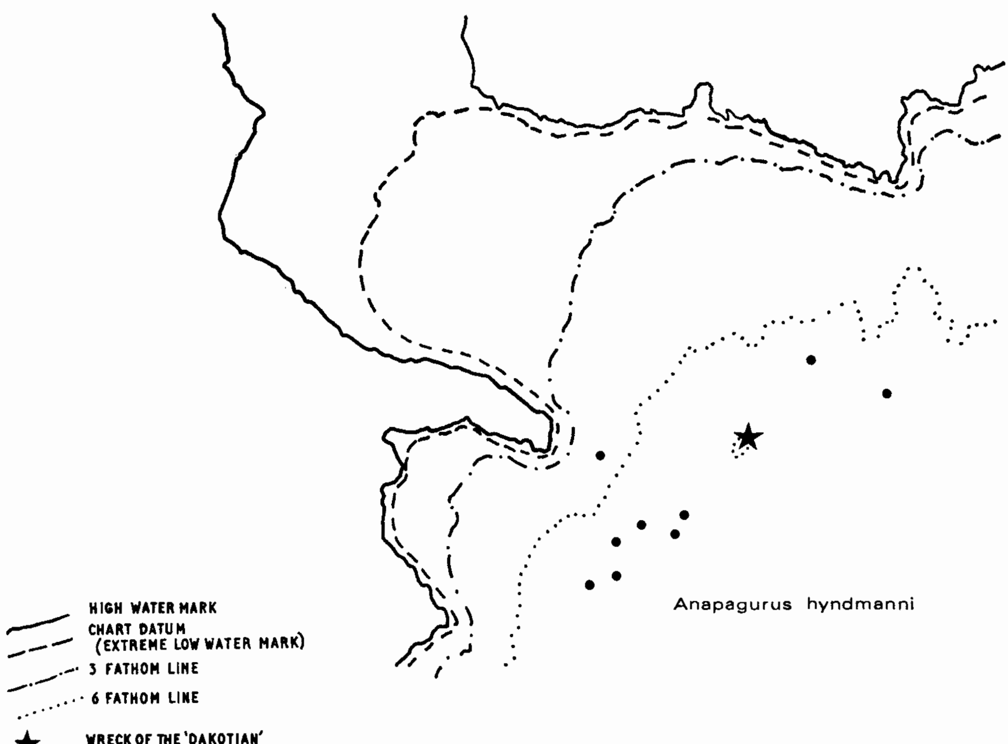
Similar food does allow the possibility of inter-specific competition for food, but this is most unlikely to restrict *Carcinus*, for intra-specific competition in shallow water must surely be far greater. The extent of this competition can be judged from the averages of between 12 and 25 crabs per trap (Table 2) and the occasional capture of more than 60 in single traps. The most extreme example of this competition encountered during the survey was as follows: a dead conger eel was found on the shore at low water, placed in an empty trap and left in the same position on the shore. Seven hours later, at high tide, the trap was lifted and found to contain 300 crabs—which must thus have entered at an average rate of one every 90 seconds. The relatively few *Carcinus maenas* that are found below the 3 fm. line are probably the aged, parasitized, or diseased individuals, who can no longer compete with healthy crabs in shallow water (see Crothers, 1968).

Factors limiting the landward distribution of the other species

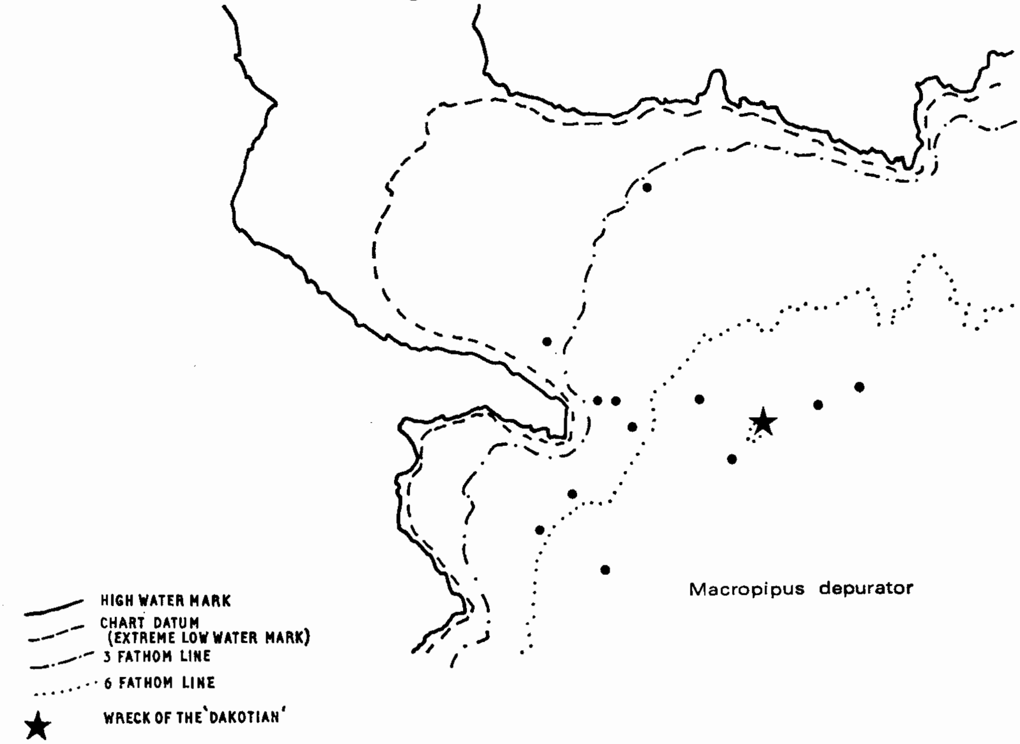
If it is a salinity factor that restricts *Carcinus maenas* to shallow water the other species can be expected to show the opposite response. None of these species can



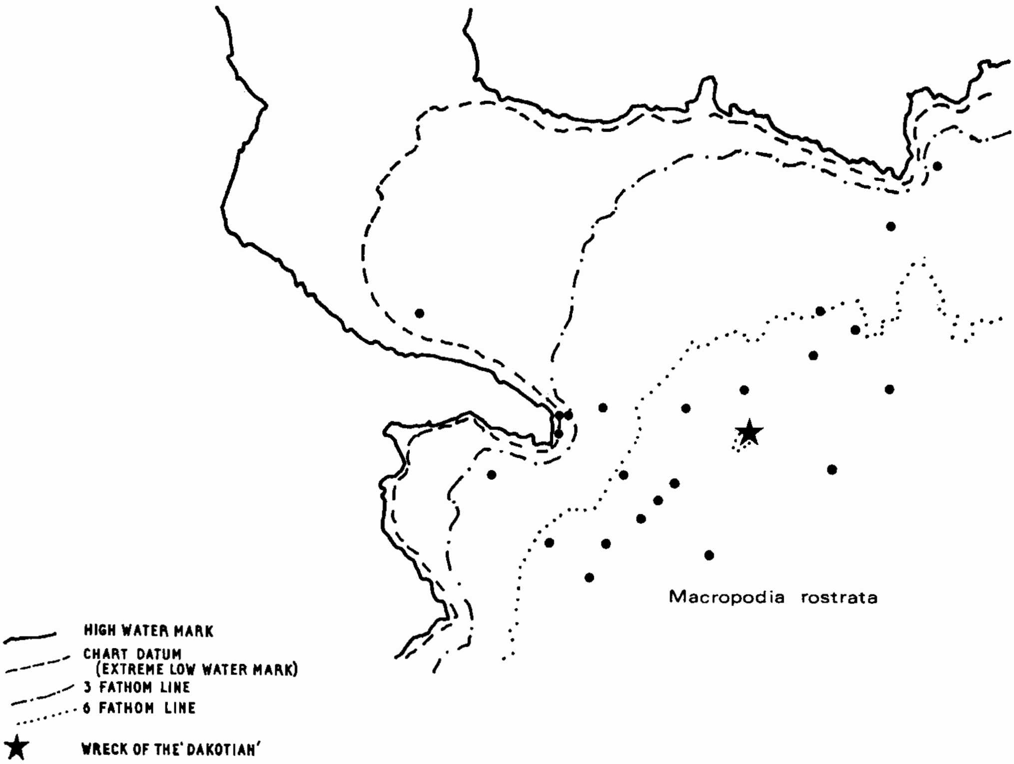
MAP 7.
Dale Roads: the distribution of *Pagurus bernhardus* in traps.



MAP 8.
Dale Roads: the distribution of *Anapagurus hyndmanni* in traps.



MAP 9.
Dale Roads: the distribution of *Macropipus depurator* in traps.



MAP 10.
Dale Roads: the distribution of *Macropodia rostrata* in traps.

live long under conditions of reduced salinity, and all are fully marine animals. Coupled with this may be an inability to compete with the dense population of *Carcinus maenas* found in shallow water. *Inachus* and *Macropodia* might even be attacked and eaten, as sometimes happens in aquaria. In either case (competition or predation) it is apparent that other species avoid concentrations of *Carcinus maenas*. To test this concept of avoidance, analysis (of 2×2 contingency tables) was made of the number of joint occurrences with *Carcinus maenas* in the traps for each of the other species. It will be noted (Table 3a) that with the exception of *Cancer pagurus* and *Macropipus depurator* the negative associations are significant. The corresponding coefficients of association are shown in Table 3b. When the same analysis is applied to other combinations of species (e.g., Table 4) there is usually a small, non-significant positive association. When comparing two rare species it is almost inevitable to show a small positive association (see Fager 1967; Southwood, 1966).

Table 3 thus bears out the contention that these species do avoid *Carcinus maenas*, and thus any factor affecting the distribution of *Carcinus* may also affect theirs.

Hermit crab distribution will be further affected by the availability of suitable shells. Small *Pagurus bernhardus* have a wide selection available but large individuals must find those of the common whelk, *Buccinum undatum* (this being the only large enough shell to occur commonly in Dale Roads). Not surprisingly, therefore, Table 4 shows a significant positive association between whelks and *Pagurus bernhardus*.

The 6 fm. Depth Zone

Inachus dorynchus was known to be an inshore species, but Hartnoll's (1963) paper had not suggested maximum abundance in such shallow water. He was unable to ascribe control of spider crab distribution to any one factor but concluded that availability of suitable food (which is correlated with the type of substrate) must have an effect. The Admiralty chart gives no indication of any major changes in the substrate over the area of Dale Roads under consideration; the whole being SSh (sand and shell) or SG (sand and gravel). Further investigations, probably by divers, will be required before this distribution pattern can be explained.

Both *Macropipus puber* and *Cancer pagurus* can be found, at low tide, on the rocky shores around Dale Roads, but almost never on the sandy Dale Beach or Gann Flat. Likewise, under water, both are thought to favour rocky areas and avoid sandy bottoms. The described food of these species (Munz *et al.*, 1965) are all rocky shore animals. It might be thought that the distribution patterns shown in Fig. 2 simply reflect the availability of rocky areas, for even the headlands drop to the sand table within the 6 fm. lime. But a glance at the maps shows this unlikely to be the total explanation for many were trapped at considerable distances from the nearest rocks. Once again further research is necessary.

Acknowledgements

I am grateful to Mr. J. H. Barrett, then Warden of Dale Fort Field Centre, for his encouragement of my work on crabs, and for sanctioning expenditure from the research fund at the Centre to purchase traps. Thanks are also due to my wife, Marilyn, for assistance in preparation of the maps and for drawing Fig. 1; and to the many people who, from time to time, assisted with the field work, often under somewhat unpleasant conditions.

Table 3. *The degree of association between* Carcinus maenas *and other species as indicated by the number of joint occurrences in 184 sub-littoral traps.*

(a) 2+2 CONTINGENCY TABLES

Notation (from Southwood 1966)

		Species A present	Species A absent	
Species B	present	a	b	a+b
	absent	c	d	c+d
		a+c	b+d	n = a+b+c+d

Species A	Species B	a	b	c	d	Association (+ or −)	χ^2	P
Carcinus maenas	Macropipus puber	9	86	20	69	—	5·244	·02
Carcinus maenas	Cancer pagurus	8	87	13	76	—	1·181	·20
Carcinus maenas	Pagurus bernhardus	36	59	60	29	—	14·54	·001
Carcinus maenas	Anapagurus hyndmanni	0	95	9	80	—	8·04	·01
Carcinus maenas	Macropipus depurator	3	92	9	80	—	2·60	·1
Carcinus maenas	Inachus dorynchus	0	95	10	79	—	9·23	·001
Carcinus maenas	Macropodia rostrata	4	91	20	69	—	11·95	·001

χ^2 was calculated from the formula given by Southwood (1966)

$$\chi^2 = \frac{n\,(\,[\,ad - bc\,] - (n/2))^2}{(a+c)\ (b+d)\ (a+b)\ (c+d)}$$

Where [ad − bc] signifies placing the term in the positive form.
The probablilities were taken from Fisher & Yates (1957).

(b) COLE'S (1949) COEFFICIENT OF INTERSPECIFIC ASSOCIATION

This coefficient is a number varying from +1 (complete positive association) through 0 (no association) to − 1 (complete negative association) and can be calculated, with its standard deviation, from one of these formulae (after Southwood 1966)

when ad $\geqq$ bc :

$$CAB = \frac{ad - bc}{(a+b)\ (b+d)} \pm \sqrt{\frac{(a+c)\ (c+d)}{n\ (a+b)\ (b+d)}}$$

when bc > ad and d $\geqq$ a

$$CAB = \frac{ad - bc}{(a+b)\ (a+c)} \pm \sqrt{\frac{(b+d)\ \ (c+d)}{n\ (a+b)\ \ (a+c)}}$$

when bc > ad and a > d

$$CAB = \frac{ad - bc}{(b+d)\ (c+d)} \pm \sqrt{\frac{(a+b)\ \ (a+d)}{n\ (b+d)\ \ (c+d)}}$$

Species A	Species B	CAB
Carcinus maenas	Macropipus puber	− 0·399 ± 0·165
Carcinus maenas	Cancer pagurus	− 0·262 ± 0·199
Carcinus maenas	Pagurus bernhardus	− 0·344 ± 0·654
Carcinus maenas	Anapagurus hyndmanni	− 1 ± 0·315
Carcinus maenas	Macropipus depurator	− 0·516 ± 0·270
Carcinus maenas	Inachus dorynchus	− 1 ± 0·296
Carcinus maenas	Macropodia rostrata	− 0·684 ± 0·190

Table 4. *The degree of association shown between other species pairs as indicated by the number of joint occurrences in sub-littoral traps. The coefficient of interspecific association is only calculated where the* χ^2 *test shows the association to be greater than would be expected by chance.*

(Notation as in Table 3)

Species A	Species B	a	b	c	d	±	χ^2	P	CAB
Pagurus bernhardus	Buccinum undatum	71	25	16	72	+	53	·001	+0·506±·668
Pagurus bernhardus	Macropodia rostrata	14	82	10	78	+	0·18	·7	
Pagurus bernhardus	Macropipus depurator	10	86	2	86	+	3·88	·05	+0·042±·0614
Pagurus bernhardus	Inachus dorynchus	3	93	7	81	–	1·25	·3	
Pagurus bernhardus	Anapagurus hyndmanni	9	87	0	88	+	6·18	·01	+0·047±0·016
Macropodia rostrata	Inachus dorynchus	5	19	5	155	+	9·5	·01	+0·146±0·575

Summary

1. This paper describes a survey of the distribution of crabs (Brachyura and Paguridea) in the shallow water of Dale Roads during summers 1964–1966.

2. The opportunity was taken to investigate the existence of one, or more, critical depth zones between 0 and 6 fm.

3. Of the thirteen species trapped, eight were sufficiently common for their distribution to be studied in detail. One, *Carcinus maenas*, predominated in shallow water but decreased abruptly in abundance below the 3 fm. line. Three species, young *Cancer pagurus*, *Macropipus puber*, and *Inachus dorynchus*, showed maximum abundance between the 3 fm. and 6 fm. lines; whilst four species, *Pagurus bernhardus*, *Anapagurus hyndmanni*, *Macropipus depurator*, and *Macropodia rostrata* showed increasing catches in progressively deeper water.

4. The results show a well-marked critical depth zone for all species at or near the 3 fm. line.

5. It is suggested that *Carcinus maenas* is restricted in the main to the shallow side of this zone by a salinity factor, and that the other species favour the other side of the zone on account of the opposite response to the salinity factor coupled with an avoidance of *Carcinus maenas* concentrations.

6. Sickly *Carcinus maenas*, forming some 4 per cent of the total population, also favour the stable, fully marine, conditions below the 3 fm. line.

7. A second, less well defined, critical zone at or near the 6 fm. line is apparent for young *Cancer pagurus*, *Macropipus puber*, and *Inachus dorynchus*. Further research is needed before this can be adequately explained.

References

Bassindale, R. and Clarke, R. B. (1960). The Gann Flat, Dale: studies on the ecology of a muddy beach. *Field Studies*, **1** (2), 1–22.

Bouvier, E. -L. (1940). Decapodes Marcheurs. Faune de France, **37**, 367 pp.. Paris.

Broekhuysen, G. J. (1936). On development, growth, and distribution of *Carcinides maenas* (L.). *Arch Néerl. Zool.*, **2**, 257–399.

Bruce, J. R., Colman, J. S., and Jones, N. S. (1963). *Marine Fauna of the Isle of Man and its surrounding seas*. 307 pp. Liverpool.

Chumley, J. (1918). *The Fauna of the Clyde Sea Area. Being an attempt to record the zoological results obtained by the late Sir John Murray and his assistants on board the S.Y. "Medusa" during the years 1884–1892.* 200 pp. Glasgow.

Cole, H. A. (1956). Benthos and the shellfish of commerce. Chapter V of Graham, M. (ed.) *Sea Fisheries: their investigation in the United Kingdom*. 486 pp. London.

Crothers, J. H. (1966). Dale Fort Marine Fauna (2nd ed.). *Field Studies*, **2**, supplement. 169 pp.

Crothers, J. H. (1968). The biology of the shore crab, *Carcinus maenas* (L.): 2. The life of the adult crab. *Field Studies*, **2**, 579–614.

Fager, E. W. (1957). Determination and analysis of recurrent groups. *Ecology*, **38**, 586–595.

Fisher, R. A. and Yates, F. (1957). *Statistical tables for biological, agricultural, and medical research.* 5th ed. 138 pp. London and Edinburgh.

Hartnoll, R. G. (1963). The biology of Manx spider crabs. *Proc. zool. Soc. Lond.*, **141**, 423–496.

Marine Biological Association (1957). *The Plymouth marine fauna*. 457 pp. Plymouth.

Muntz, Louise, Ebling, F. J., and Kitching, J. A. (1965). The ecology of Lough Ine XIV. Predatory activity of large crabs. *J. Anim. Ecol.*, **34**, 314–329.

Naylor, E. (1958). Tidal and diurnal rhythms of locomotory activity in *Carcinus maenus* (L.). *J. Exp. Biol.*, **35**, 602–610.

Naylor, E. (1962). Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. *J. Anim. Ecol.*, **31**, 601–609.

Selbie, C. M. (1921). The decapoda reptantia of the coasts of Ireland. II. Paguridea. *Fisheries, Ireland, Sci. Invest.*, 1921.

Southwood, T. R. E. (1966). *Ecological methods with particular reference to the study of insect populations.* 389 pp. London.