

THE BIOLOGY OF THE SHORE CRAB

CARCINUS MAENAS (L.)

2. THE LIFE OF THE ADULT CRAB

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INTRODUCTION

The Shore Crab, *Carcinus maenas* (L.), is one of the best known of all intertidal animals, being common, relatively large, and easily found. The readiness with which it is identified, sexed, measured, and marked suggests its suitability for field study.

The mass of published work about this animal is split between specialized physiological studies on the one hand and the often superficial statements in popular accounts of the shore on the other. This paper aims at the middle position and reviews the literature in the light of current work at Dale Fort with a view to suggesting where further research might be particularly rewarding.

The first part of the paper (Crothers, 1967) reviewed the anatomy, growth, and life history of this crab, and this second part, describing the life of adult crabs, will continually refer to the background established there. After a consideration of field techniques the life of the crab will be described under three headings: distribution in space and time; relations with other species; and survival on the shore.

FIELD TECHNIQUES

The field data presented in this paper were obtained during 1963–1966 whilst the author was Assistant Warden at Dale Fort Field Centre, situated at the south-western tip of Wales (Map 1). Recent descriptions of the physical features of the area around the Centre and of its fauna and flora have been published (for example: Moyse and Nelson-Smith, 1963; Nelson-Smith, 1965, 1967; Crothers, 1966; Jones and Williams, 1966) and further description here would be superfluous.

It is appropriate, before examining the results of this work, to consider the field techniques used to acquire the data.

C. maenas can be collected by hand on the shore at low tide but to sample under water an aqualung or some type of net or trap is required. Crabs can be dredged and trawled, but these methods lack precision and cannot be used in rocky areas. They are occasionally taken on lines and even, exceptionally, in plankton nets but most investigators have used baited traps. Clearly the designs employed have varied but the Leakey "Universal" trap, fitted with $\frac{1}{2}$ inch mesh courlene netting (Fig. 1), has proved very successful at Dale. The in-

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genious method of retaining the catch within the trap cannot seriously restrict the entry of active crabs for on several occasions catches of more than 60 crabs in single traps were obtained; and once 300 were taken.

Almost any animal remains will serve as bait to attract crabs—rotting *Conger* and dead chicken proving the most spectacular—the major problem being to keep the bait uniformly attractive.

Baited trapping presents its own disadvantages as a sampling method, for only the active, hungry crabs are caught and the numbers taken can be expected to vary inversely with the naturally available food supply. Crabs do not normally feed during the period of the moult (say D_2 to B_2 in the notation used by Crothers, 1967) and so are unlikely to be taken in traps at this time. D_2 to B_2 occupies some 18–20 per cent of the moult cycle so this means that individual crabs are only trappable for 80 per cent of the time and, as there is no fixed moulting season for *C. maenas* (Crothers, 1967), may mean that only 80 per cent

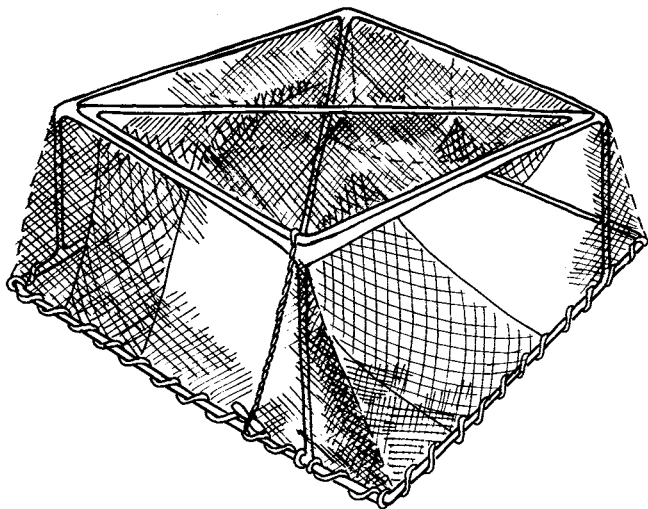
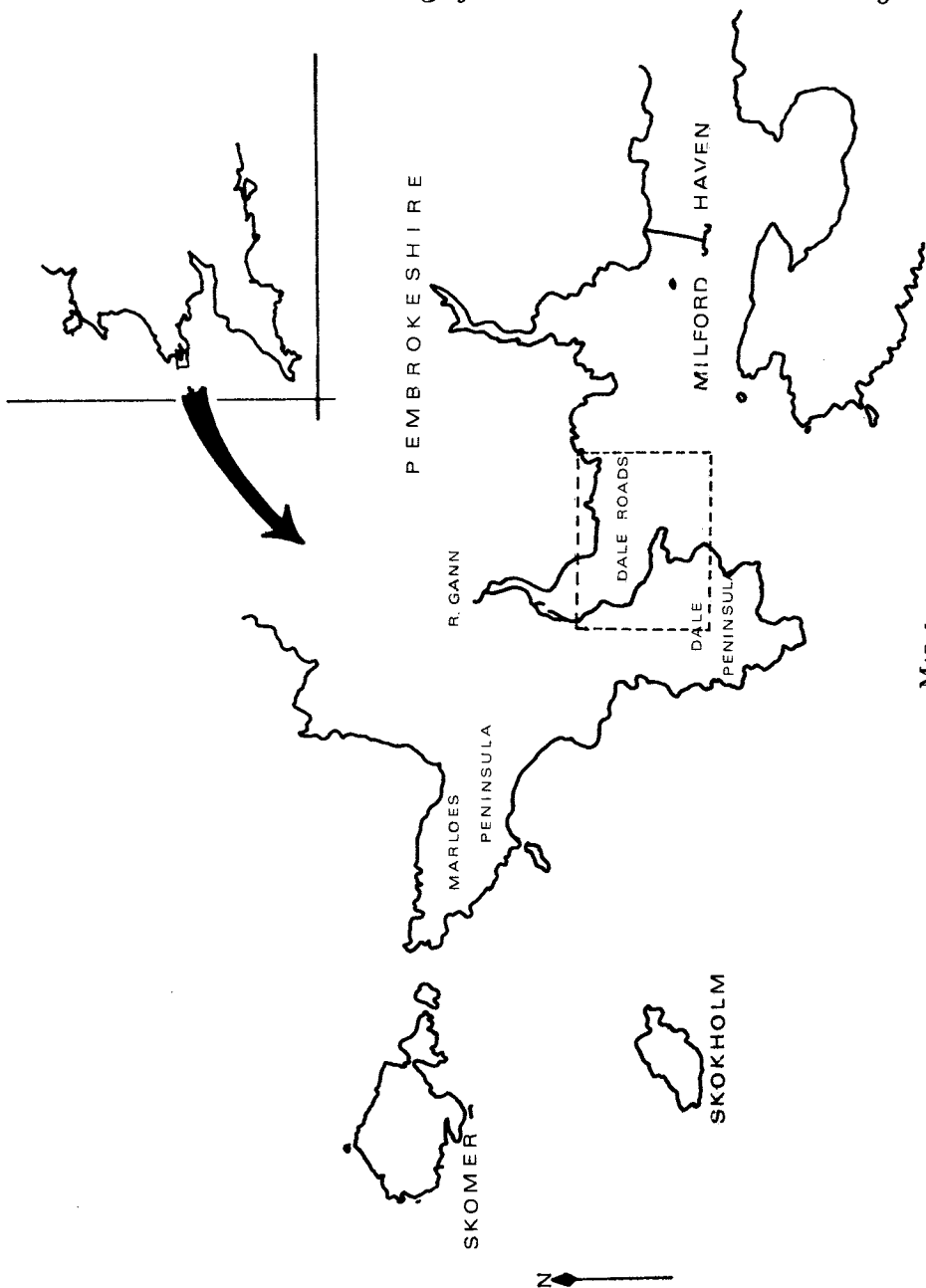


FIG. 1.

The Leakey "Universal" Trap (manufactured by R. and B. Leakey, Settle, Yorkshire).

of the total population can be caught at any one time. Furthermore, paired crabs (in-copula or pre-copula), parasitized, and berried crabs are unlikely to enter traps as readily as "normal" individuals on account of their reduced mobility. Occasionally some of these are caught, but most must remain unsampled.

Many quantitative techniques require the marking, release, and recapture of individuals. The marks must permit repeated recognition in the field but must not render the crab more conspicuous (either to would-be predators or to the collector) nor alter its way of life. The conventional methods of marking arthropods by painting the surface (in any case usually unsuccessful unless the

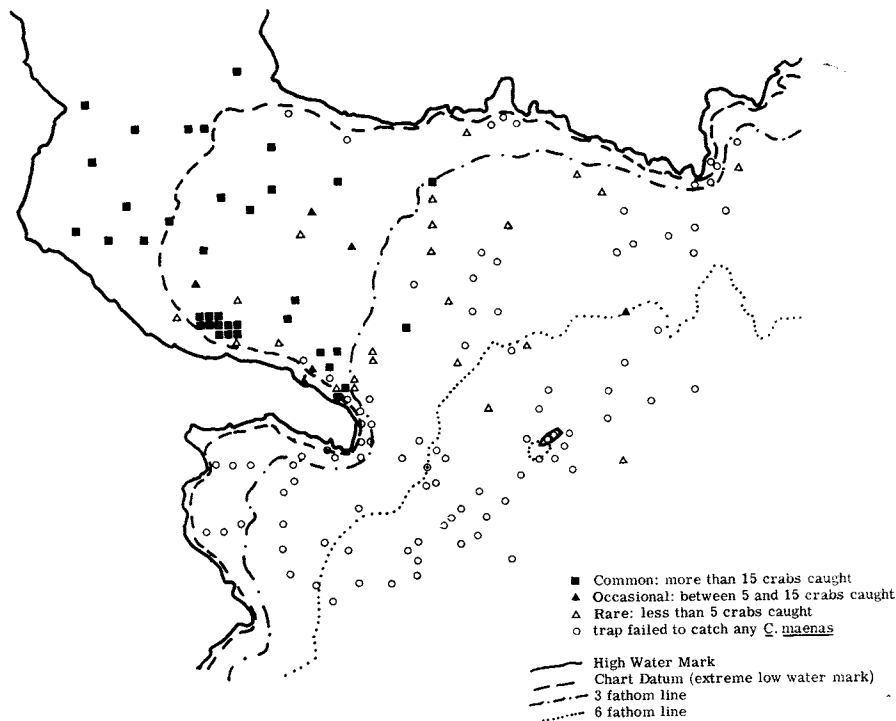


MAP 1.

South-west Pembrokeshire, showing the position of the Dale Peninsula at the mouth of Milford Haven. The dotted rectangle indicates the area studied by trapping and the boundaries of Maps 2, 6 and 7.

animal's surface is dry at the time of application) or attaching tags to the legs are unsatisfactory in that the mark is lost when the crab moults. The same disadvantage attends Edwards' (1958) technique—used for the Dale work—of clipping the antero-lateral teeth on the carapace. Clearly long-term experiments are impossible with any of these methods, but by concentrating on adult crabs—which moult much less frequently than juveniles (Crothers, 1967)—and limiting the experiment to a few days, it is hoped that few errors were incurred.

A far better technique was described by Edwards (1965) for *Cancer pagurus* in which a numbered tag is inserted into the pleural groove in such a way that it is retained at the moult. As far as I am aware this technique has yet to be modified to suit *C. maenas*, but when it is it should open up many fields of long-term investigation.



MAP 2.

Distribution of *C. maenas* in Dale Roads, July to September, 1964-1966. Each symbol represents the result of at least one trap-night.

DISTRIBUTION IN SPACE AND TIME

Geographical

C. maenas is a European Atlantic species recorded from Morocco to the North Cape, the Faeroes, and southern Iceland (Bouvier, 1940; Broekhuysen, 1936). The allied *C. mediterraneus* Czerniavsky, recently separated from *C. maenas* on several grounds (see Demeusey, 1958; Holthuis and Gottlieb, 1958; Naylor, 1961, 1965) is found throughout the Mediterranean and extends through the Suez Canal to reach the Red Sea (Holthuis and Gottlieb, 1958).

C. maenas is also present along the east coast of America from Nova Scotia to Virginia (Holthuis and Gottlieb, 1958), probably as a result of introductions. *Carcinus* (species undetermined) has in addition been recorded from: the Bay of Panama (Rathbun, 1930); Willapa Bay, Washington (Ricketts and Calvin, 1962); Pernambuco, Brazil (Rathbun, 1930); Australia (McNeil, 1953); Hawaii (Rathbun, 1930); and Ceylon (Holthuis and Gottlieb, 1958).

Table 1. *Analysis of female C. maenas trapped in Dale Roads, July to September 1964-1966. The figures in brackets indicate the (additional) number of crabs visibly infected by Sacculina carcini.*

Size	Depth taken			
	on the shore	0-3 fm.	3-6 fm.	below 6 fm.
70	0 (0)	3 (0)	0 (0)	0 (0)
60	31 (0)	150 (2)	13 (0)	0 (0)
50	256 (0)	408 (15)	48 (1)	0 (0)
40	218 (4)	182 (24)	15 (2)	1 (0)
30	201 (2)	12 (10)	1 (0)	0 (0)
20	74 (0)	2 (1)	0 (0)	0 (1)
Total	780 (6)	757 (52)	77 (3)	1 (1)
Add—for un-measured crabs	(2)	43	(1)	
Total	780 (8)	800 (52)	77 (4)	1 (1)

Size Groupings: carapace breadth was measured in millimetres, and individuals grouped into tens. Thus size 20 includes crabs with carapace breadth between 15.0 mm. and 24.9 mm.; size 30 all those between 25.0 mm. and 34.9 mm., etc.

Local distribution in summer

Shore crabs are not confined to the shore. Edwards (1958) deduced and Naylor (1962) demonstrated that many of the large crabs move up and down the shore with the tide. But all individuals do not take part in this "migration" and each day the crab population will be divided between the three sections that I shall call "A", "B" and "C". Individuals are able to move freely between the sections but some crabs must spend days, weeks, or even years in the same one.

Table 2. *Analysis of male C. maenas trapped in Dale Roads, July to September 1964-1966.* The figures in brackets indicate the (additional) number of crabs visibly infected by *Sacculina carcini*.

Size	Depth taken			
	on the shore	0-3 fm.	3-6 fm.	below 6 fm.
70	4 (0)	8 (0)	0 (0)	0 (0)
60	22 (0)	59 (0)	2 (1)	0 (0)
50	113 (1)	71 (11)	3 (1)	0 (0)
40	138 (2)	26 (11)	1 (2)	0 (1)
30	105 (0)	4 (8)	0 (9)	0 (1)
20	84 (0)	0 (1)	0 (0)	0 (0)
Total	466 (3)	168 (33)	6 (13)	0 (2)
Add—for un-measured crabs	(1)	5 (3)		
Total	466 (4)	173 (36)	6 (13)	0 (2)

Size groupings as in Table 1.

Table 3. *Analysis of all C. maenas trapped in Dale Roads, July to September 1964-1966.* The figures in brackets indicate the (additional) number of crabs visibly infected by *Sacculina carcini*.

Size	Depth taken			
	on the shore	0-3 fm.	3-6 fm.	below 6 fm.
70	4 (0)	11 (0)	0 (0)	0 (0)
60	53 (0)	209 (4)	15 (1)	0 (0)
50	369 (1)	479 (26)	51 (2)	0 (0)
40	356 (6)	208 (35)	16 (4)	1 (1)
30	306 (2)	16 (18)	1 (9)	0 (1)
20	158 (0)	2 (2)	0 (0)	0 (1)
Total	1,246 (9)	925 (85)	83 (16)	1 (3)
Add—for un-measured crabs	(3)	48 (3)	(1)	
—for unsexed crabs	482			
Grand total	1,728 (12) 1,740	973 (88) 1,061	83 (17) 100	1 (3) 4

Size groupings as in Table 1.

Section A crabs spend low tide hidden under cover on the shore, emerging to search for food as the tide covers them and hiding again before the ebb.

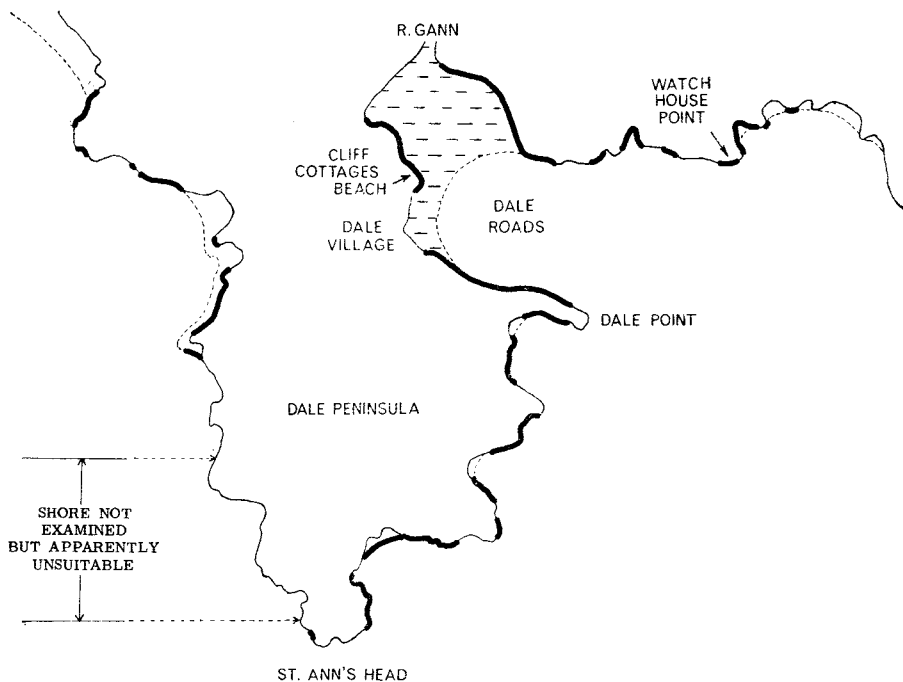
Section B crabs spend low tide beneath the tidemarks but feed on the shore at high tide; coming up the shore with the flood and moving back on the ebb.

Section C crabs spend all 24 hours beneath the tidemarks.

Thus all crabs found on the shore at low tide belong to section A; those trapped on the shore at high tide belong to section A or B; and those trapped beneath the tidemarks to section B or C.

Section A crabs

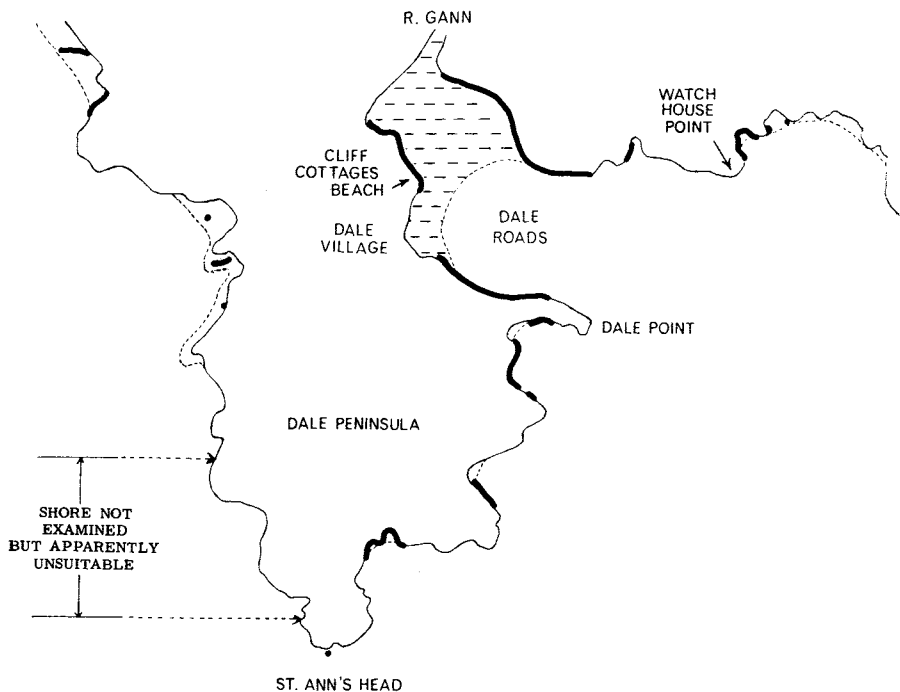
First-year crabs (up to 34 mm. carapace breadth, i.e. up to size 30 in Table 1) form a large proportion of section A. Many (?most) of them spend all their time on the shore. Crabs of this size have been taken in traps at Dale—although many size 20 must escape—and Tables 1–3 show that whilst many were taken on the shore few were caught sub-littorally and most of those were parasitized by *Sacculina carcini* and must therefore have been at least one year old (see p. 601).



MAP 3.

Distribution of young (up to 25 mm. carapace breadth) *C. maenas* on the shore at low tide around the Dale peninsula. August 1965–1966.

The young crabs may be found at low tide in summer on many shores around the Dale peninsula (Map 3), usually under stones covered with green algae where local shelter allows shingle to accumulate—although the cover of fucoids or mussel byssi is equally suitable when available. On many of these shores it is only the young crabs that are found at low tide, and, whilst individual *C. maenas* may occasionally appear on almost any shore, the adults are usually confined



MAP 4.

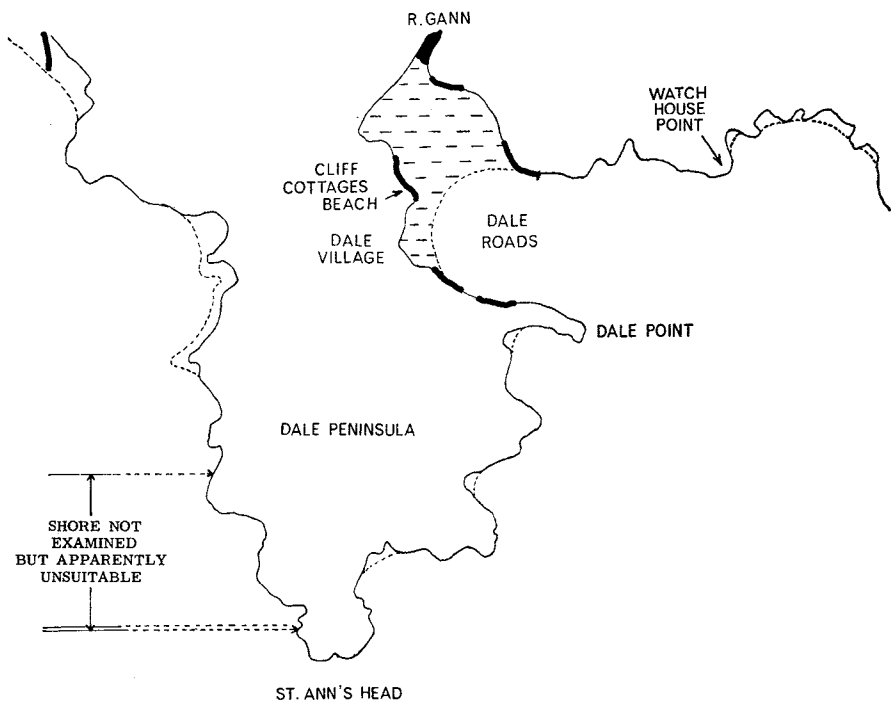
Distribution of medium-sized (25-50 mm. carapace breadth) *C. maenas* on the shore at low tide around the Dale peninsula, August 1965-1966.

(at low tide) to those shores (Maps 4 and 5) which bear a good cover of fucoids or an abundance of large stones and boulders to provide shelter. The correlation between the distribution pattern of young adult *C. maenas* (Map 4) and that of the egg wrack, *Ascophyllum nodosum*, in Jones and Williams (1966), should not pass unnoticed.

Where adults do occur on the shore at low tide they may be present in considerable numbers. A short mark-release-recapture experiment on a 100 yd. stretch of one such shore (Cliff Cottages, Dale: Fig. 2) in October, 1963, suggested daily totals of between 1,700 and 4,500 crabs (calculated by Fisher's and Ford's (1947) method after Parr (1965)). Gaskell and Parr (1966) esti-

mated the total population on the whole of this shore (500×70 yards) in September 1966, at 250,000 with considerable daily fluctuations.

Edwards (1958) described a mark-release-recapture experiment on section A adults found in three small isolated rocky areas on an otherwise sandy/muddy shore in Southampton Water. His results show a preponderance of males (67 per cent) and a high recapture rate suggesting that many crabs return to the same area of rocks on subsequent low tides. Wells (1965) doubts reports of homing in decapod crustacea and it was partly to check whether this "homing" of *C. maenas* was a normal behavioural pattern, or one imposed on the South-



MAP 5.

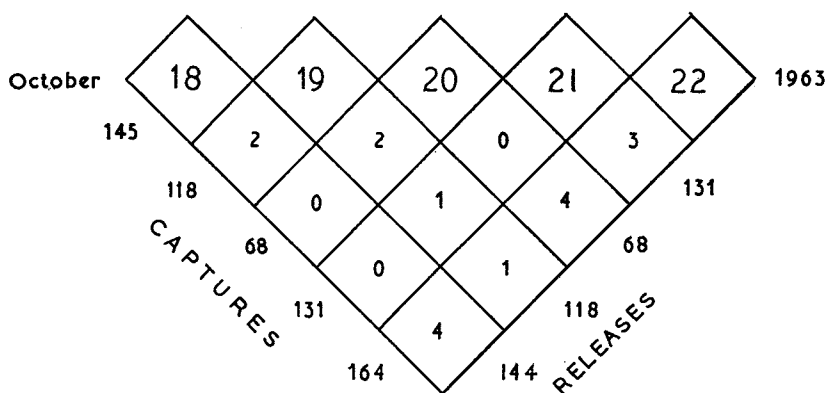
Distribution of large (more than 50 mm. carapace breadth) *C. maenas* on the shore at low tide around the Dale peninsula, August 1965-1966.

ampton crabs by a shortage of suitable cover, that the short experiment (mentioned above) was performed at Dale. Once again a preponderance of males (81 per cent) was noted, but there was no evidence of homing. In his first five days Edwards caught 382 males of which 50 (13 per cent) were recaptures whereas the 626 males taken in 5 days at Dale included only 17 (2.7 per cent) recaptures. On the beach at Dale the same hiding places were searched each day; they usually harboured comparable numbers of crabs but only once was an individual recaptured near its original position.

Most Section A crabs are found on rocky shores within the range of neap

tides. Occasionally they will shuffle into the sand or mud if no other cover is available but they do not normally dig a burrow. It is thus perhaps surprising that so many *C. meanas* should colonize salt marshes—above high water of neap tides and thus not submerged every day—and excavate permanent burrows in the banks of drainage channels. The channel banks of the Gann salt marsh, Dale, are riddled with burrows that interconnect to form complex galleries running back at least 18 inches into the bank. In July 1965 a section of bank was excavated and all the crabs caught and measured (Table 4). The majority were small, first-year size individuals (although the burrow entrances were large enough for adults) and of nearly equal sex ratio.

MALES



FEMALES

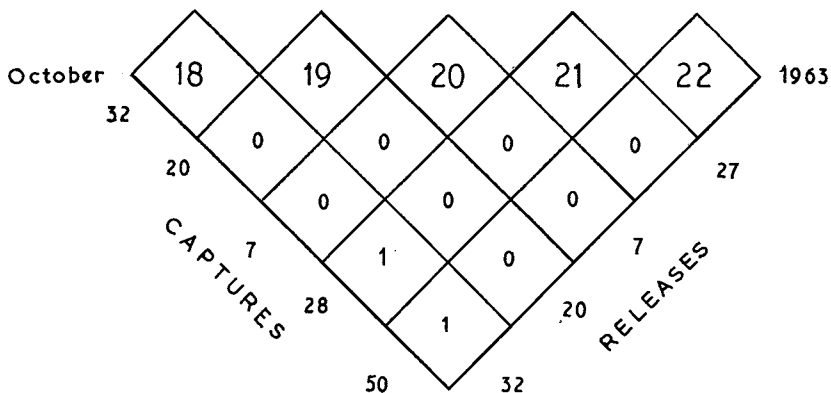


FIG. 2.

A mark-release-recapture experiment of section A. Crabs on 50 square yards of Cliff Cottages Beach, Dale.

Table 4. A comparison between crabs dug, at low tide, from their burrows along 30 feet of drainage channel bank and crabs trapped at high tide in the same area. Gann Salt Marsh, Dale, July, 1965.

Sizes	Crabs from their burrows		Crabs trapped	
	Males	Females	Males	Females
70	0	0	2	0
60	0	0	8	14
50	5	4	108	185
40	15	9	134	194
30	35	53	104	193
20	41	40	83	74
Totals	96	106	439	660

The same data (but ignoring the size 20 crabs, which can escape from traps) expressed as percentages to show the differences in size frequency more clearly:

Sizes	Crabs from burrows		Crabs in traps	
	Males	Females	Males	Females
70	0	0	1	0
60	0	0	2	2
50	9	6	30	32
40	27	14	38	33
30	64	80	29	33
	100	100	100	100

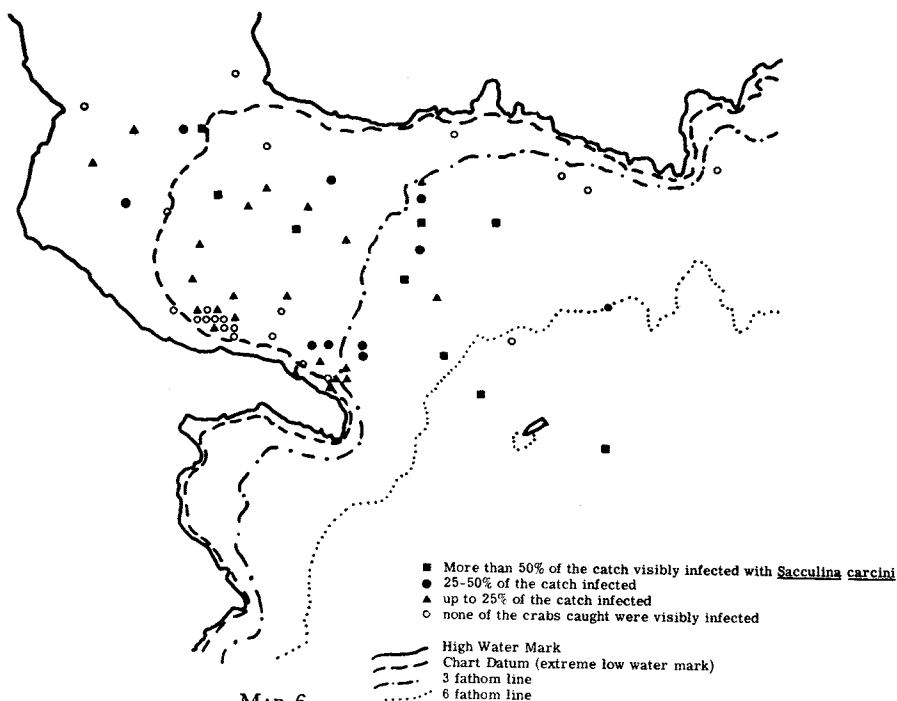
Section B crabs

The crabs trapped at high tide on the salt marsh (Table 4) clearly represent a different section of the population from those found there at low tide. If the invaders, which can be observed moving up the drainage channels with the flood tide, have come from below the low tide mark they have travelled a thousand yards across the shore. Evidence for such movement comes from occasional capture on the marsh of a crab bearing living *Balanus crenatus*, a barnacle that cannot withstand upper shore conditions.

It is not easy to separate crabs belonging to section B from section C crabs when examining the catch from sub-littoral traps. However, there are a few indicators available.

(i) *Distance from the shore.* It is unlikely that section B crabs will move far below low tide mark, yet *C. maenas* can be found at some distance from the shore (Map 2). I suspect that all those taken below about 3 fm. fall into section C, whilst section B crabs will predominate just below the tidemarks.

(ii) *Parasitization.* Crabs parasitized by *Sacculina carcini* occasionally appear on the shore, but Tables 1-3 show that (at Dale) they are more frequent offshore. These data, presented again more clearly in Table 5, confirm earlier



MAP 6.

Distribution of sacculinized *C. maenas* in Dale Roads, July to September 1964-1966, as shown by trapping.

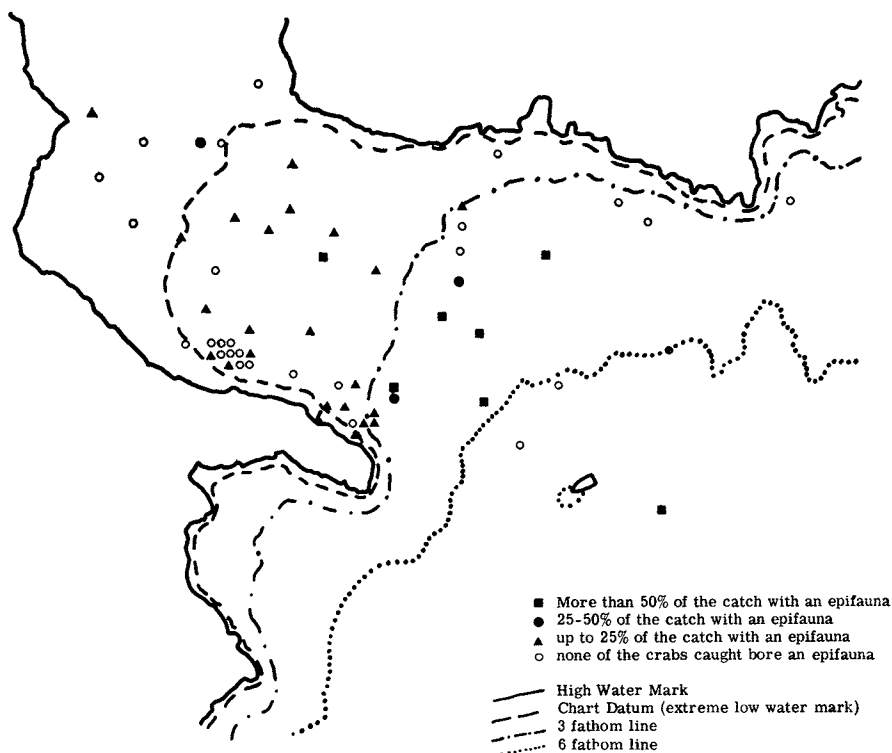
impressions (e.g. of Rasmussen, 1959) that sacculinized crabs move offshore. The proportions of parasitized crabs recorded are minimal values, for these animals are less active than healthy individuals (and so less likely to be trapped) and the parasite may be affecting the crab's behaviour before there is any external evidence of infection. The positions in which sacculinized crabs were trapped in Dale Roads (Map 6) suggest that most of them must be in section C, and the paucity of captures on the shore (most of which were only just above chart datum) would seem to confirm this.

Table 5. *Distribution of sacculinized C. maenas trapped in Dale Roads, July to September, 1964-1966.*

	On the shore	0-3 fm.	3-6 fm.	below 6 fm.
Number of crabs trapped (Table 3)	1,740	1,061	100	4
Number infected	12	88	17	3
% infected	0.7	8	17	(75)

(iii) *Epizoids*. Tables 1-3 also show that the larger (older) crabs figure more prominently offshore, but that there is no appreciable size difference between crabs from different sub-littoral depths (in summer). Some of these older crabs, which moult at long intervals or have ceased moulting (see Crothers, 1967) bear algae and an epifauna of encrusting animals on carapace and legs. When the distribution of such crabs is summarized (Map 7; Table 6)—and again these are minimal values for few crabs were closely examined for newly settled organisms—it will be seen that they predominate in deeper water, and thus may be more typical of section C than B. The occasional trapping of these crabs on the shore is direct proof of section B movement (see above).

(iv) *Colour*. Body colour may provide another indicator of past habitat (see also p. 608) for adults vary from light green to dark red. An attempt to assess the colours of crabs collected by hand on the middle shore (section A), trapped



MAP 7.

Distribution of crabs bearing epizoic animals in Dale Roads, July to September 1964-1966, as shown by trapping.

Table 6. *Distribution of crabs bearing epizoic animals trapped in Dale Roads, July to September, 1964-1966.*

				MALES			
				On the shore	0-3 fm.	3-6 fm.	below 6 fm.
Number of crabs trapped							
(from Table 2)	470	209	19	2
Number bearing an epifauna	0	17	3	1
% bearing an epifauna	0	8	16	(50)
				FEMALES			
				On the shore	0-3 fm.	3-6 fm.	Below 6 fm.
Number of crabs trapped							
(from Table 1)	788	852	81	2
Number bearing an epifauna	3	75	31	0
% bearing an epifauna	0.4	8	38	(0)
				TOTAL			
				On the shore	0-3 fm.	3-6 fm.	Below 6 fm.
Number of crabs trapped	1,258	1,061	100	4
Number bearing an epifauna	3	92	34	1
% bearing an epifauna	0.2	8	34	(25)

at high tide on the lower shore (sections A plus B) and trapped sub-littorally (sections B and C) is reported in Table 7. The assessment was, of necessity, subjective but the results suggest that the proportion of predominantly green individuals increases up the shore (and salt marsh crabs are almost all greenish) whilst that of predominantly red crabs increases offshore (most specimens from deeper water being more or less red).

The continual movement of individuals between the sections blurs all distinctions and prevents certain assignment of a specimen to any one section. But it does appear that large, red crabs with an epifauna and/or the parasite *Sacculina* are typical of section C; whilst healthy green crabs with no encrusting growths (except of filamentous green algae) are probably in section A. Section B crabs are intermediate.

Section C crabs

It was noted in the previous section that section C crabs are found further offshore than the rest of the population. At Plymouth (Marine Biological Association, 1957) and Swansea (Naylor, 1962) the seaward limit of *C. maenas* is given as 3 fm. At Dale, in summer, some crabs have been taken below 6 fm.

Table 7. *Variations in the colour of adult C. maenas from different habitats around Dale.*

MALES						
	Total no. of crabs caught	Number predominantly		%		
		green	red	green	red	
Middle shore	609	512	95	84	16	
Lower shore	30	21	9	70	30	
Sub-littoral (0-3 fm.) ..	135	85	50	63	37	

FEMALES						
	Total no. of crabs caught	Number predominantly		%		
		green	red	green	red	
Middle shore	138	132	6	96	4	
Lower shore	94	60	34	63	37	
Sub-littoral (0-3 fm.) ..	512	213	299	40	60	

TOTAL						
	Total no. of crabs caught	Number predominantly		%		
		green	red	green	red	
Middle shore	747	646	101	86	14	
Lower shore	124	81	43	65	35	
Sub-littoral (0-3 fm.) ..	647	298	349	46	54	

(Map 2) but 96 per cent of the 2,904 crabs trapped were within the 3 fm. line (Table 3). Some individuals occasionally move deeper, as shown by records, from 11-18 fm. in the southern North Sea (Broekhuysen, 1936) and 30 fm. in the Firth of Clyde (Chumley, 1918) but the species remains an essentially coastal one.

Variations in activity during the day

Shore crabs are not continually active throughout the 24 hour cycle but show bursts of activity interspersed with periods of quiescence. These bursts follow a pattern that has been interpreted (Naylor, 1958) as representing two cycles of activity, one associated with the tides and the other with the day-night cycle.

Their combined effect makes the crabs active at high tide and at night, with twice-monthly peaks of maximum activity when high tide occurs near midnight. A drop in temperature, such as would be experienced by a section A crab on being covered by the tide (in summer) also stimulates a burst of activity. This stimulation, recurring with a tidal frequency, may serve to reinforce the endogenous rhythm (Naylor, 1963)—see also p. 609. Both adults (Naylor, 1958) and juveniles (Powell, 1962*b*) exhibit the two rhythmical patterns in tidal areas,

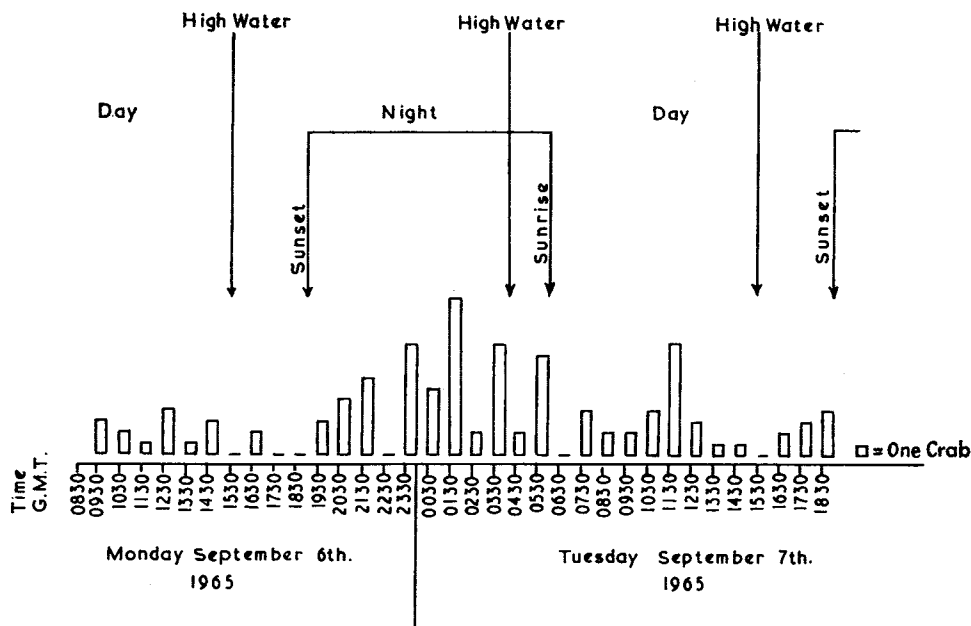


FIG. 3.

The feeding activity of some sub-littoral *C. maenas* as shown by their time of entry into a single trap laid, in about 2 fm. of water, off the Dale Fort jetty. The trap was visited at hourly intervals and the catch released at least 15 feet away.

but crabs collected from non-tidal conditions (Swansea Docks) show the day/night cycle only (Naylor, 1960).

During the periods of reduced activity—at low tide and by day—section A crabs tend to hide away under cover, but some sub-littoral crabs may continue to forage for food. Fig. 3 shows the results of lifting and emptying a single trap at hourly intervals over a 32 hour period. Maximal activity occurred as expected during the hours of darkness but some crabs continued to enter by day. Aqualung dives in the area by day failed to find any foraging *C. maenas*.

Seasonal changes in local distribution

The foregoing sections have described the summer (April–October) distribution, when the majority of the adult population is in section B with section A second, and section C—composed mainly of the halt and lame—last. This pattern, deduced by Edwards (1958) and first demonstrated by Naylor (1962) is best shown by the Dale data when the latter are expressed (Table 8) in terms of mean trap effort.

During the autumn there is a gradual move offshore of adults from sections A and B into C. Naylor (1962) believes the crabs to remain within the 3 fm. limit in contrast to Edwards' (1958) suggestion of a general move into deeper water. The winter data for Dale (Table 8) suggest a swelling of numbers in the 0–3 fathom zone but are insufficient to permit the winter range to be plotted.

From December to March section A disappears, except for some (?all) first year crabs (Edwards, 1958; Naylor, 1962). In some places and some years—e.g. Swansea, 1960–1961 (Naylor, 1962)—section B, although present in both December and March, apparently disappeared in January and February. In other places and other years—e.g. Dale, February/March, 1964—section B persisted, although with reduced numbers (Table 8) and reduced range. The crabs trapped on the shore at this period (Table 9) must all be section B, for none could be found there at low tide. It is noticeable that berried females and sacculinized crabs of both sexes usually remain in section C.

Naylor (1963) has shown temperature to affect the movements of *C. maenas*. His suggestion that the move back onshore in March/April is temperature

Table 8. *Variation in the abundance of C. maenas trapped at different depths in Dale Roads, in terms of mean trap effort.*

Depth trapped:	Summer (July–September 1964–1966)			
	On the shore	0–3 fm.	3–6 fm.	Below 6 fm.
(1) Number caught	1,740	1,061	100	4
(2) Number of trap/periods	71	90	47	47
Mean catch	25	12	2	0.08

Depth trapped:	Winter (January–March 1964–1965)	
	On the shore	0–3 fm.
(3) Number caught	112	446
(2) Number of trap/periods	26	21
Mean catch	4	21

Notes.

- (1) Totals from Table 3.
- (2) Trap periods were usually trap-nights, but occasionally bad weather prevented collections in deeper water, mostly near the mouth of Dale Roads.
- (3) Totals from Table 9, +6 unsexed crabs.

Table 9. *Relative distribution of C. maenas trapped in Dale Roads during winter (January-March 1964-1965).*

[] Before the entry shows the (additional) number of berried females.
 () After the entry shows the (additional) number sacculinized.

Size range	MALES		FEMALES	
	Shore	0-3 fm.	Shore	0-3 fm.
70	1	6 (1)	0	0
60	3	39 (1)	2	[2] 34 (1)
50	10	62 (3)	13	[5] 116 (10)
40	17 (1)	20 (5)	[1] 25 (1)	[3] 58 (19)
30	12	1 (2)	12	[1] 8 (8)
20	4	2 (1)	4	0
Grand total	47 (1) 48	130 (13) 143	[1] 56 (1) 58	[11] 216 (38) 303
% berried females			2	5
% sacculinized crabs ..	2	10	2	12.5

controlled was confirmed by the apparent rarity of the crab in spring 1963 following an unusually cold winter (see Crisp, 1964).

Superimposed on these possibly temperature-controlled movements are changes associated with breeding and moulting. Pairing crabs occur in section A, can be found on the shore at low tide, and have (twice at Dale) been taken from traps set on the shore at high tide—but never in traps offshore. Females move offshore in autumn before the males (which may in part account for the preponderance of males in Fig. 2) and most remain in section C until their eggs hatch. The less common "summer cycle females" (bearing eggs in spring and summer—see Crothers, 1967) may stay in section B, or even A, for salinity variations will be less serious at the higher temperatures (Broekhuysen, 1936). At Dale the summer cycle seems unimportant for only 2 out of the 1,658 unparasitized adult females trapped were in berry.

Moulting crabs are often seen in section A (though very rare in traps); their restricted movement will prevent their joining section B; and there are no data for section C.

Long term movements

It appears that the megalopa larva settles on the shore and that the young crab remains there (i.e. in section A) until the following spring. Once adult it usually joins section B in summer, often withdrawing to section C for the winter. It probably repeats this cycle for at least two seasons, at sizes 40 and 50. Older crabs, i.e. in the fourth year, in (or approaching) terminal anecydysis, usually become less active and eventually remain in section C all the time—although some individuals of size 60 can still be taken in section B.

Very few really large crabs were taken in the Dale, or Lough Ine (Muntz *et al.*, 1965) trap series—none approaching the 86 mm. carapace breadth attained by the largest Plymouth crabs (Carlisle, 1957). Naylor (1962) noticed a decline in the numbers of the largest crabs in August and suggested that the old crabs

Table 10. *Organisms known to have been eaten by C. maenas, with a few that are apparently not eaten.*

Organism	Eaten						Not eaten
	In aquaria			In the field			
	Living	Shell cracked	Dead	Living	Dead	Bait in traps	
Coelenterates					0
<i>Actinia equina</i>					3
<i>Bunodactis verrucosa</i>					3
<i>Tealia felina</i>					3
<i>Anemonia sulcata</i>					3
Sipunculoids					3
Annelids							
Nereidae	3	3				
<i>Nephtys</i>	3	3				
<i>Eulalia</i>	3	3				
Terebellidae	(if very hungry)					
<i>Lumbricus</i>	3					
Crustacea							
Amphipods	3	3				
Isopods	3	3				
<i>Crangon</i>	3	3	1			
<i>Palaemon</i>	3	3	1			
<i>Palaemonetes</i>	3	3				
crabs	3	3				
zoeae (<i>Maia</i>)	3					
Mollusca							
<i>Patella</i>	3				3	
<i>Monodonta</i>	3					
<i>Gibbula</i>	6		6			
<i>Littorina</i>	3					
<i>Nucella</i>	4		4			
<i>Helix</i>						3
<i>Anomia</i>						6
<i>Mytilus</i>	4	3	4			
<i>Enis</i>	3				3	
<i>Ostrea</i>			2, 8			7
Pectinidae	3 (small)		2			
Myidae			2			
<i>Lutraria</i>	3					
<i>Cardium</i>	3	3				
<i>Venerupis</i>	3					
<i>Scrobicularia</i>	3					
Echinoderms							
<i>Asterias</i>						5
<i>Paracentrotus</i>	6		6			
Vertebrates							
"Fish"				1		
Fish fry			1			
<i>Scylliorhinus</i>					3	
<i>Conger</i>					3	
<i>Onos</i>	3	3				
<i>Gaidropsarus</i>	3	3				
<i>Morone</i>					3	
<i>Scomber</i>					3	
<i>Gobius microps</i>	3	3				
<i>Blennius</i>	3	3				
"Fowl"					1	
"meat" (offal, etc.)					3	

References: (1) Bell (1853); (2) Buchsbaum and Milne (1960); (3) Crothers (unpublished); (4) Ebling *et al.* (1964); (5) Hancock (1955); (6) Muntz *et al.* (1965); (7) Walne (1961); (8) Yonge (1960).

die off at this season—which would explain their absence from the Dale and Lough Ine data, both taken in August/September.

RELATIONS WITH OTHER ANIMALS

Food

C. maenas eats a wide variety of living and dead animal matter. Table 10, listing organisms known to have been eaten by the crab, is undoubtedly incomplete and may be inaccurate, for organisms accepted in aquaria are not necessarily eaten in the sea. The table also lists a few animals that are apparently not eaten. There will be many more of these: animals that the crab (*a*) cannot catch, (*b*) cannot break open, or (*c*) finds distasteful.

Potential prey is detected at a distance through the water by sense organs on the antennae (see Crothers, 1967, for references). The crab makes apparently random searching movements with its legs and chelae. Funnel canals on the tips of the appendages respond quickly to the touch of any food substance, and the crab jumps on its prey, pinning it to the ground. A worm is held by the chelae whilst the third maxillipeds guide it towards the mouth. When presented with a broken-open mollusc the crab tears lumps off with its chelae and passes them to the mouth parts. A crab that has lost both chelae anchors the carcass with its legs and tears off the food with its maxillipeds.

Living molluscs or sea urchins must be cracked open before the meat is accessible (see Ebling *et al.*, 1960; Muntz *et al.*, 1965). Only small (young) topshells, mussels, and urchins are vulnerable to *C. maenas* but dogwhelks of all sizes, especially the thin-shelled form, may be broken by the larger crabs. Most of these animals are crushed by the master chela, but sometimes the smaller chela can be inserted between the valves of a bivalve or be used to chip away at the aperture of a gastropod. Occasionally the crab removes *Nucella* from its shell complete. *Nucella* shells that are too solid to crush may be abandoned by the crab after a few chips at the aperture (Ebling *et al.*, 1960). Chipped shells may thus indicate crab activity, but unfortunately birds, especially gulls, also leave chipped shells on the shore (Moore, 1938).

Many more data are required before any assessment can be made of the effect (if any) of available food supplies on the numbers and movements of *C. maenas*; or, for that matter, of the effect of a large crab population on a potential prey species. Such a common animal must exert a considerable effect. In Lough Ine present information (Ebling *et al.*, 1960; Muntz *et al.*, 1965) suggests that the crab may control mussel, urchin, and dog whelk distribution, so it is surprising that many recent publications on shore ecology (e.g. Lewis, 1964; Moyse and Nelson-Smith, 1963; Nelson-Smith, 1967) should omit reference to this animal.

Predators

Table 11 lists the animals recorded as feeding on *C. maenas*, or on "crabs" in circumstances that suggest that this species would be involved. Even though crab remains from stomachs and stomach pellets (e.g. of gulls) can often be identified to species, the list is far from complete and may well include other small wading birds and corvids that feed on the shore. Which predator kills the most crabs is hard to assess; amongst birds it may be the herring gull (*Larus*

Table 11. *Predators of C. maenas.*

Key					
A—often eaten.		B—occasionally eaten.		C—has eaten in the laboratory.	
D—suspected of eating.		X—does not eat <i>C. maenas</i> .			
Species	<i>C. maenas</i> mentioned		<i>C. maenas</i> implied		Does not eat crabs
	adult	larva	adult	larva	
Invertebrates					
Most plankton feeders				D (3)	
Various crab species	B (3)	C (3)			
<i>Octopus vulgaris</i> (Common octopus) ..	C (16)		B (23)		
<i>Eledone cirrhosa</i> (Lesser octopus) ..			B (23)		
<i>Sepia officinalis</i> (Cuttlefish) ..			B (23)		
Fish					
<i>Anguilla anguilla</i> (Common eel) ..	A (10, 19)				
<i>Blennius pholis</i> (Common blenny) ..	C (3)				
<i>Callionymus lyra</i> (Dragonet) ..	A (10)				
<i>Clupea harengus</i> (Herring) ..				A (10, 19)	
<i>Clupea sprattus</i> (Sprat) ..				A (19)	
<i>Conger conger</i> (Conger eel) ..	A (19)		A (4)		
<i>Cottus bubalis</i> (Father lasher) ..	B (19)				
<i>Cottus scorpius</i> (Sea scorpion) ..			B (4)		
<i>Crenilabrus melops</i> (Gilt head) ..	B? (10)				
<i>Gadus callarias</i> (Cod) ..	B (10, 19)				
<i>Gadus luscus</i> (Pout) ..	A (10)		A (4)		
<i>Gadus merlangus</i> (Whiting) ..	A (10)	A (15)		A (19)	
<i>Gadus minutus</i> (Poor cod) ..					X (10)
<i>Gadus pollachius</i> (Pollack) ..					X (10)
<i>Galeorhinus galeus</i> (Tope) ..			A (4)		
<i>Gobius paganellus</i> (Rock goby) ..	B (10)				
Other <i>Gobius</i> sp. ..					X (10)
<i>Limanda limanda</i> (Dab) ..	A (10)				
<i>Morone labrax</i> (Bass) ..	A (5), B (10)				
<i>Mustelus mustelus</i> (Smooth hound) ..			A (4)		
<i>Platyichthys flesus</i> (Flounder) ..	A (10, 13)				
<i>Pleuronectes platessa</i> (Plaice) ..	B (10)				
<i>Raia</i> sp. (Rays) ..			D (23)		
<i>Scophthalmus maximus</i> (Turbot) ..			A (4)		
<i>Scyliorhinus canicula</i> (Dogfish) ..	A (5)				
<i>Trigla lineata</i> (Streaked gurnard) ..			A (4, 23)		
Birds					
<i>Actitis hypoleucos</i> (Common sandpiper) ..	A (24)				
<i>Alle alle</i> (Little auk) ..			A (24)		
<i>Anas platyrhynchos</i> (Mallard) ..	B (17, 24)		B (2)		
<i>Ardea cinerea</i> (Heron) ..			B (24)		
<i>Aythya marila</i> (Scaup) ..			A (24)		
<i>Botaurus stellaris</i> (Bittern) ..			B (24)		
<i>Bucephala clangula</i> (Goldeneye) ..			A (24)		
<i>Calidris alpina</i> (Dunlin) ..			A (24)		
<i>Calidris canutus</i> (Knot) ..			A (24)		
<i>Clangula hyemalis</i> (Long-tailed duck) ..			A (24)		
<i>Colymbus arcticus</i> (Black-throated diver) ..			A (24)		

(continued overleaf)

(continued overleaf)

Species	<i>C. maenas</i> mentioned		<i>C. maenas</i> implied		Does not eat crabs
	adult	larva	adult	larva	
<i>Colymbus immer</i> (Great northern diver)	A (24)				
<i>Haematopus ostralegus</i> (Oystercatcher)			A (24)		
<i>Larus argentatus</i> (Herring gull)	A (7, 9, 14, 22)		A (24)		
<i>Larus fuscus</i> (Lesser black-backed gull)			B (24)		X (9)
<i>Larus hyperboreus</i> (Glaucous gull)			A (24)		
<i>Larus marinus</i> (Greater black-backed gull)	B (9)		A (24)		
<i>Limosa lapponica</i> (Bar-tailed godwit)			A (24)		
<i>Melanitta fusca</i> (Velvet scoter)			A (24)		
<i>Melanitta perspicillata</i> (Surf scoter)			A (24)		
<i>Mergus serrator</i> (Red-breasted merganser)			A (24)		
<i>Numenius arquata</i> (Curlew)			A (24)		
<i>Numenius phaeopus</i> (Whimbrel)			A (24)		
<i>Phalacrocorax aristotelis</i> (Shag)	A (12)				
<i>Phalacrocorax carbo</i> (Cormorant)	B (24)				
<i>Podiceps griseigena</i> (Red-necked grebe)			B (24)		
<i>Somateria mollissima</i> (Eider)	A (24)				
<i>Somateria spectabilis</i> (King eider)	A (24)				
<i>Squaterola squaterola</i> (Grey plover)			A (24)		
<i>Tadorna tadorna</i> (Shelduck)			A (24)		
<i>Tringa flavipes</i> (Yellowshank)			A (24)		
<i>Tringa nebularia</i> (Greenshank)			A (24)		
<i>Tringa totanus</i> (Redshank)			A (24)		
<i>Turdus musicus</i> (Redwing)			B (24)		
<i>Uria grylle</i> (Black guillemot)			B (24)		
Mammals					
<i>Halichoerus grypus</i> (Grey seal)			B (11, 12)		
<i>Homo sapiens</i> (Man)	A/B (20, 1)				
<i>Kogia breviceps</i> (Pygmy sperm whale)	B (8)				
<i>Lutra lutra</i> (Otter)	B (6)				
<i>Phoca vitulina</i> (Common seal)	B (18)				

Note 1. The decision whether or not to include fish known to feed on "crabs" was based largely on records of fish (Crothers, 1966) within the known range of *C. maenas* (Map 2).

Note 2. It was presumed that *C. maenas* was the most likely crab to be available to birds, for most of these species catch crabs on the shore and few will dive to depths greater than 3 fathoms.

References: (1) Bell (1853); (2) Campbell (1947); (3) Crothers (unpublished); (4) Day (1880-1884); (5) J. W. Donovan (personal communication); (6) Elmhirst (1938); (7) Goethe (1956); (8) Harmer (1927); (9) Harris (1965); (10) Hartley (1939); (11) Lockley (1966); (12) Lumsden (1946); (13) Markowski (1966); (14) Meijering (1954); (15) Nagabhushanam (1964); (16) Nixon (1966); (17) Olney (1964); (18) Sergeant (1951); (19) Scott (1902); (20) Schmitt (1965); (21) Southern (1964); (22) Tinbergen (1953); (23) Wilson (1935); (24) Witherby *et al.* (1938-1941).

argentatus Pont.) as both Goethe (1956) and Meijering (1954) found that they fed principally on *C. maenas* at some times of the year, whilst both Tinbergen (1953) and Harris (1965) found that they took more *C. maenas* than other crab species. Analysis of gull pellets—especially for chelae—would show the size range of the crabs swallowed whole; but to this must be added the larger crabs which are dismembered on the shore and from which the gull swallows the meat only. My impression is that herring gulls feed mostly on young adult crabs but the data are so incomplete as not to be worth including here. Cormorants and shags also take large and medium sized crabs, but most other avian predators are recorded as taking small crabs. The heaviest predation from birds is thus probably on section A crabs plus or minus one year old.

Modern man collects *C. maenas* more for bait than for food. In Britain the species is now hardly eaten at all although Bell (1853) was able to write: "This crab is much eaten by the poorer classes on the coast and great numbers are also brought to the London markets; the flavour being very tender and sweet." In the United States the species is eaten in restaurants and the annual catch for food totals between 60 and 70,000 pounds (Schmitt, 1965, p. 193).

Parasites

The known parasites of *C. maenas* are listed in Table 12 and, with the exception of *Sacculina carcini* (which alone betrays its presence externally), very little is known about them.

Under favourable conditions *S. carcini* breeds throughout the year, mainly in summer and autumn, showing slight seasonal variation with latitude. The eggs are retained by the adult until they hatch into typical cirripede nauplii. The nauplius moults to a cypris larva which sinks to the bottom and settles, during the night, on the integument of a small crab, attaching itself by the first antenna (Caullery, 1952). The parasite moults off the cyprid skeleton and appears as a tiny blob from which develops a thin chitinous dart-shaped tube which is forced through a weak point in the crab's integument (e.g. the basal articulation of a hair) and through which the parasite injects itself into the host. Those cyprids that do not settle near a weak point in the integument die.

The parasite grows and develops a network of threads which ramify through the body of the host to absorb food. In so doing it delays the accumulation of food reserves within the crab and consequently the latter's moult cycle (Passano, 1960; see Crothers, 1967). When the host moults again, perhaps nine months after infection, the parasite is nearly mature and appears externally under the abdomen.

On first appearance the visceral mass (or externa) is small, 1–4 mm. long, and white in colour; but it soon grows and darkens. The externa is an elongated sac usually attached near the base of the crab's abdomen, forcing it open in the same way as the female crab's egg plug unfolds her abdomen; although the parasite externa is never as large as an egg plug. It contains a nerve ganglion and two small testes but most space is occupied by ovaries which shed their products into the central (pallial) cavity, opening externally by a visible pore (Caullery, 1952). Crabs with young, white, externae can be found throughout the year but are most numerous in August/September, implying maximum

Table 12. *Parasites of C. maenas*.

References				
Species	Phylum	Life cycle	Stage attacking crab	Recorded from
description				
classification				
locality				
<i>Carcinonemertes carcinophila</i>	Nemertini	Egg—pilidium-like larva— young worm; development on crab; young worms may move to a new host or stay on parental crab	Young on gills, adult within egg plug of crab; those on a male crab can- not mature	Holland (62% inf.) Belgium Plymouth Woods Hole (U.S.A.)
				10 12 14
				1 2 13 14
<i>Fecampia erythrocephala</i>	Platyhelminthes	Egg—larva enters crab—when mature leaves crab and lays eggs in cysts on rocks—dies	Developing stages in haemocoel	Plymouth (cysts) Isle of Man (adults, cysts)
				10 3 13
<i>Microphallus similis</i> (= <i>Cercaria ubiquita</i>) (= <i>Spelotrema excellens</i>)	Platyhelminthes	Adult in gulls; cercaria in gastropods (<i>Littorina saxatilis</i> and <i>Hydrobia ulvae</i>): metacercaria in crabs (almost always <i>C. maenas</i>)	Encysted metacercariae in digestive gland—and probably other tissues: probably does little harm to the crab	Plymouth (cercaria) Dale (all stages) Anglesey (adult) Swansea (adult)
				6 9 13

<i>Portunon maenadis</i>	Arthropoda (Isopoda)	Egg—epicaridean larva (looks like normal isopod) in surface plankton: microniscan larva parasitic on Copepods: cryptoniscan larva, free living, enters crab: adult	Adult in crab haemocoel—can be found especially under hypodermis of mouth parts. Dwarf male in brood pouch of female	Plymouth Exmouth	4	13 17
<i>Sacculina carcini</i>	Arthropoda (Cirripedia)	Egg—planktonic nauplius larva: cypris larva settles on crab: adult in crab	Adult permeates whole body of host: becomes visible externally as yellow/brown, non-granular lump	Roscoff Plymouth Dale Colwyn Bay Morecambe Bay Clyde Isle of Wight	4 7 8 11 13 15 19	5 6 7 8 11 13 15 19
<i>Thelothania maenadis</i>	Protozoa (Sporozoa)	Apparently entire life cycle within one crab	Especially in striated muscle	Bassin d'Arachon (Bordeaux)	16 (13)	16

References: (1) Anon (no date); (2) Broekhuysen (1936); (3) Bruce *et al.* (1963); (4) Caullery (1952); (5) Chumley (1918); (6) Crothers (1966); (7) Delage (1884); (8) Foxon (1939); (9) Harris (1964); (10) Hyman (1951); (11) James and Marshall (1952); (12) MacGinitie and MacGinitie (1949); (13) Marine Biological Association (1957); (14) McIntosh (1873); (15) Orton (1936); (16) Perez (1904); (17) Perkins (1924); (18) Rothschild (1940); (19) Rydal School (no date).

infection in November/December. The externa steadily darkens from white through shades of yellow, grey, and brown. All dark brown externae are more than six months old (Foxon, 1939), i.e. 15 months after infection.

Two or more parasites in one host would mean less food for each and a greater chance of the host dying before completion of the parasite life cycle. The developing *S. carcini* secretes a toxin which circulates in the haemolymph of the crab (Florkin, 1960) and presumably kills later infectors. The very occasional double or triple infections may be the result of simultaneous attack on the host by two (or three) cyprids, neither (none) of which is able to assert mastery over the other(s). Examples of similar mechanisms for reducing intra-specific competition are known amongst insect parasitoids (Salt, 1961).

When *Sacculina* parasitises *Macropipus holsatus* the externa shrivels and drops off after a short breeding season, leaving a blackened scar and stump (Day, 1935). *C. maenas* may often be found with similar scars but Foxon (1939) suggests a different cycle in this species. Sacculinised crabs are found throughout the year and some with dark brown externae are found with encrusting organisms proving (in the Clyde) that they have not moulted for up to a year. Foxon thus suggests that the externa persists for a considerable time, producing larvae whenever the conditions are favourable. Occasionally it may suffer accidental damage and fall off, leaving the blackened scar, but Foxon suspects that they can be regenerated (although in aquaria damage to the externa usually leads to the death of the crab). The cycle might be different in Denmark for Rasmussen (1959) noted behavioural differences between crabs with externae and those with scars. No differences in distribution were apparent in Dale Roads.

A much documented effect of *S. carcini* is the modification of the male host towards the female condition. The effect of the parasite is that of removing the androgenic gland (Charniaux-Cotton, 1960; see Crothers, 1967). In a normal male the sustained allometric development of secondary sexual characters is due to high concentrations of the androgenic hormone. The parasite removes this hormone and stimulates the gland to such excessive secretion and enlargement that it finally degenerates. Loss of the hormone means loss of all male characters, including spermatogenesis, but of course the external features cannot change until the moult. At the next (last) moult the external characters of the crab revert towards the female form, the degree of reversion presumably indicating the state of the androgenic gland at the time of moult. All degrees of change, from slight alterations in the proportions of the legs to complete femaleness (setous pleopods in place of styles, seven jointed abdomen, etc.) can be found in all sizes of host. But the larger the crab the less liable he is to modification, and the smaller he is the greater the amount of modification that may occur (Foxon, 1939).

Changes in behaviour match the changes in appearance (e.g. Rasmussen, 1959). The sacculinised crab behaves to its externa as a female does to her egg plug, carrying out all the cleaning and airing movements and usually adopts the protective "eischutsreflex" on being handled. The offshore movement of sacculinised and berried crabs was noted on p. 590.

The occurrence of dark brown externae on small (first year size) crabs, and white externae on large (fourth year size) hosts requires explanation if, as Caullery (1952) claims, only small crabs are infected. Delage (1884) claims that

the undifferentiated blob can remain in an embryonic state within the crab for 20 months—but this in no way explains why it sometimes develops immediately and at other times is delayed.

Associates

As noted on p. 591 the integument of older crabs often becomes encrusted with organisms (Table 13). They probably do little harm to the crab until they

Table 13. *The epifauna that may encrust the integument of some C. maenas.*

Species (4)	Breeding season	Settlement	Longevity
Protozoa: Vorticellidae			
<i>Zoothamnium hydrobiae</i>			
Annelida: Serpulidae			
<i>Pomatoceros triqueter</i>	all year (mainly March/April) (5)		
<i>Spirorbis tridentatus</i>	summer	summer/autumn (3)	
<i>Spirorbis pagenstecheri</i>	summer	summer/autumn (3)	
Crustacea: Balanidae			
<i>Balanus crenatus</i>	Feb.-Nov.	April-Aug.	18 months (1)
<i>Elminius modestus</i>	all year but at a reduced rate in winter	all year but minimal in early spring (1)	
Mollusca: Mytilidae			
<i>Mytilus edulis</i>	April-June (5)	June-August (2)	
Mollusca: Anomiidae			
<i>Anomia ephippium</i>			
Chordata: Ascidiidae			
<i>Ascidella scabra</i>	May-November (5)		
Chordata: Molgulidae			
<i>Molgula manhattensis</i>	all year (5)		
Chordata: Styelidae			
<i>Botryllus schlosseri</i>	June-November (5)		
<i>Botrylloides leachi</i>	July-October (5)		

References: (1) Bassindale (1964); (2) Bayne (1964); (3) Crisp, Bailey and Knight-Jones (1967); (4) Crothers (1966); (5) Marine Biological Association (1957).

seriously increase its weight or impede movement. Organisms having a short period of settlement each year provide the investigator with an indication of the minimum time elapsed since the last moult. In the Clyde *Balanus crenatus* is particularly useful, for a crab bearing this barnacle has not moulted since April and one bearing two generations not for more than a year. In southern Britain the barnacle's breeding season is extended and it is not a useful indicator (of crab moulting) at Dale.

Competitors

The Dale Fort Marine Fauna (Crothers, 1966) lists 29 other crab species in localities where at least some *C. maenas* are found. Many of them (especially other Portunidae; and see Muntz *et al.*, 1965) will eat similar food so there is a possibility of interspecific competition for food. Data from the trapping pro-

gramme in Dale Roads show (Crothers, in prep) that the various species have slightly different habitat preferences that serve to keep them apart. Essentially *C. maenas* is a crab of sheltered rocky shores, estuaries, and sheltered shallow offshore water. It is replaced in more exposed rocky areas (on and off-shore) by *Macropipus puber*, *Cancer pagurus*, *Pilumnus hirtellus* and *Xantho incisus*; on sandy bottoms by *Corystes cassivelaunus* or *Portunus latipes* and other *Macropipus* species, especially *M. depurator* and *M. holsatus*.

In Dale Roads *C. maenas* was by far the most abundant species trapped. It can be argued (Crothers, in prep.) that if there was any competition between species *C. maenas* would be more likely to restrict the distribution of the other species than vice versa, and that it is highly probably that intra-specific competition is much more important—witness the 300 crabs in a single trap entering at a rate of one every 90 seconds.

SURVIVAL ON THE SHORE

C. maenas is distinguished from other British crabs by its adaptation to the shore habitat. This section considers some of the more important adaptations.

Tolerance of Semi-Terrestrial Conditions

When Section A crabs are trapped at low tide in small pools in which the oxygen concentration is rapidly reduced, they come to the edge of the pool and raise their fronts so that the anterior opening of the gill chambers is above the surface of the water. The scaphognathites beat normally and a stream of water can be seen running out of the opening. When the beat is reversed (Arudpragasam and Naylor, 1964a) air is pumped into the gill chambers and oxygenates the water inside, some of it emerging through the same opening and the rest through Milne Edwards' opening (in either case producing the familiar bubbling noise).

Crabs in burrows on a salt marsh will not be covered by the sea every tide. Some burrows contain pools of water but many do not and the crabs must remain out of water for several days at a time over neap tides. I have kept a young crab in moist air for ten days without ill-effect so that provided the air in the burrows remains damp and cool the crabs should survive. The galleries excavated (see p. 588) were usually damp to touch and appreciably cooler (19° C. decreasing inwards to 15·5° C.) than either the air outside (21–22° C.) or the water in a nearby drainage channel (22° C.).

Other British crabs do not usually come above mean tide level (many never come on the shore at all) and most species die in a few hours out of water. Survival depends on efficient gaseous exchange. Out of water the gill chambers fill with air (crabs that have been kept out of water float when put back in). If the gills dry out the lamellae collapse, greatly reducing the surface available for gaseous exchange, and the crab dies.

Foreign semi-terrestrial crabs (e.g. *Grapsus*, *Ocypode*, *Potamon* and *Uca*) retain some water in their gill chambers when on land and aerate it by vigorous beating of the scaphognathite (Wolvekamp and Waterman, 1960). Perhaps *C. maenas* can do likewise, whilst other British crabs are perhaps unable to retain sufficient water in their gill chambers.

Tolerance of Reduced Salinity

Crustacea evolved in the sea and developed a physiology to function in sea water. The body fluids (haemolymph and urine) of a normal marine crustacean are at the same concentration as (isosmotic to) the sea water and the integument, especially over the gills, is permeable to both salts and water. When such an animal is placed in brackish (or fresh) water it swells up with water entering the body by osmosis from the medium. To counter this involuntary uptake some animals can increase the volume of urine excreted, but in so doing they excrete a fluid more concentrated than that entering by osmosis (the urine is isosmotic to the haemolymph not to the medium) and the ionic concentration within the body falls. Unless the animal can make good this loss it will die, for most animal tissues can function normally only within a narrow range of ionic concentrations.

There are a number of recent reviews (e.g. Potts and Parry, 1964) and simple accounts (e.g. Lockwood, 1963) for those who would read further on this subject.

C. maenas, unlike other British crabs, is able to tolerate a wide range of external salinities (from 4‰ to 34‰ or higher: Broekhuysen, 1936) because it can maintain its internal (haemolymph) concentration above that of the medium and because its tissues continue to function down to an ionic concentration equivalent to 60 per cent sea water. Maintenance of a haemolymph concentration above that of the dilute medium is assisted by a reduced permeability to salts and water as compared with other British crabs, but still requires the active uptake of ions (Na^+ , K^+ , Ca^{++} , and Cl^-) from the medium to make good losses by diffusion and excretion. But even in full sea water some uptake is necessary to maintain the ionic steady state between haemolymph and medium (see Crothers, 1967) so that the crab has a mechanism for active uptake, only requiring increased efficiency to function under estuarine conditions.

Uptake requires the expenditure of metabolic energy—witness the increased oxygen consumption of the crab in dilute media (Florkin, 1960)—and energy used in staying alive is energy not available for finding food or escaping from predators. Consequently crabs with other demands on their resources, e.g. females in berry and parasitized crabs, do not usually enter brackish water or stay on the shore in section A; and all crabs find it harder to survive there in winter.

There is a maximum rate of ionic uptake (Shaw, 1961). If the rate of ionic loss exceeds the rate of uptake the animal dies. *Carcinus* cannot live long in fresh water.

The ability to withstand brackish conditions is an important prerequisite for life on the shore and is not merely an adaptation to estuarine life, for heavy rain at low tide can quickly dilute any pool. Section A crabs may always have to withstand short periods of nearly fresh water.

Protective Coloration

C. maenas is camouflaged, and the camouflage changes with the behavioural pattern of the crab. Living in a more variable environment than other British

crabs it is also more variable in colour. The dark green adult on the shore hides in dark green light under the fucoids. The red individuals from deeper water (see p. 592) will appear dark brown in a dark brown environment (for red light is almost completely absorbed in the surface 5 m. of the sea; Levring, 1966). Small individuals on the shore often show dazzle patterns of red, black and white patches on a green background which makes them hard to distinguish amongst gravel and shell fragments. *Cancer pagurus*, the next commonest "shore" crab, occasionally shows disruptive white patches when small, but never to the same extent.

The visible colour of the crab is due to chromatophores and/or the pigmented layers of the cuticle. In larval (Pautsch, 1961) and young crab (Powell, 1962a) stages the chromatophores are all-important. The three monochromatic types—red, white and black—show (1) a background (albedo) response with the black chromatophores expanding on a dark background, (2) a temperature response in which the crab becomes lighter with increasing temperature, and (3) a day/night response making the animal darker by day and lighter by night.

These responses can be observed in all small crabs but the time required for change increases with age (size) from half an hour to several days. Moreover, as the chromatophores lie in the hypodermis, they become masked by the increasing thickness of cuticle overlying them. No changes can be observed in dark individuals more than 35 mm. across, although some responses are still possible in yellow/green crabs but may take several days (Stephenson and Stewart, 1946). In most adults the chromatophores remain fully expanded (Powell, 1962a; Stephenson and Stewart, 1946).

The early crab stages (but not the megalopa) show a definite "juvenile pattern" of light and dark bands across the legs (Powell, 1962a). All young *C. maenas* show this pattern irrespective of habitat, but those from light backgrounds (sandy shores) retain it longer—up to a carapace width of 25 mm.—than those from darker, rocky shores in which it often disappears long before they reach 15 mm.

Adults cannot use their chromatophores to change colour but slow pigment changes are still possible in the outer layers of the cuticle. These outer layers may be eroded away in old crabs revealing the white calcified layer, which confirms that sub-cuticular pigments cannot affect external colour. A melanin-like pigment is responsible for black, but most of these body colours are produced by carotenoids. The pure pigments give reds, whilst browns, greens, and blues result from combinations with proteins to give carotenoproteins or chromoproteins (Nicol, 1960). On boiling or preservation (in alcohol or formalin) the carotenoprotein breaks down and releases the red pigment.

Carotenoids can only be synthesized by plants. The crab maintains its supplies by eating other organisms containing carotenoids, but it can modify the pigments by oxidation once they have entered the body (Fisher *et al.*, 1954; Goodwin, 1960). The pigment is stored in the hepatopancreas, giving it a strong orange colour in healthy crabs. If a crab is deprived of carotenoids, or if all available supplies are in use elsewhere in the body (e.g. in the eggs), the hepatopancreas loses its colour. Formation and breakdown of chromoproteins is under hormonal control from an eyestalk hormone. The chromoproteins

dissociate on removal of the eyestalks and the crab then turns red (Goodwin, 1960). Perhaps the same thing happens to crabs kept under reduced light—section C crabs. The possibility exists for a mechanism in the eyestalk to control the red/green balance of the crab's body colour in response to the light intensity of the environment.

The origin of those white patches (other than where the pigmented layer has been worn away) on the carapace is not so easily explained. American *C. maenas* with asymmetrical white patches, apparently under genetic control and

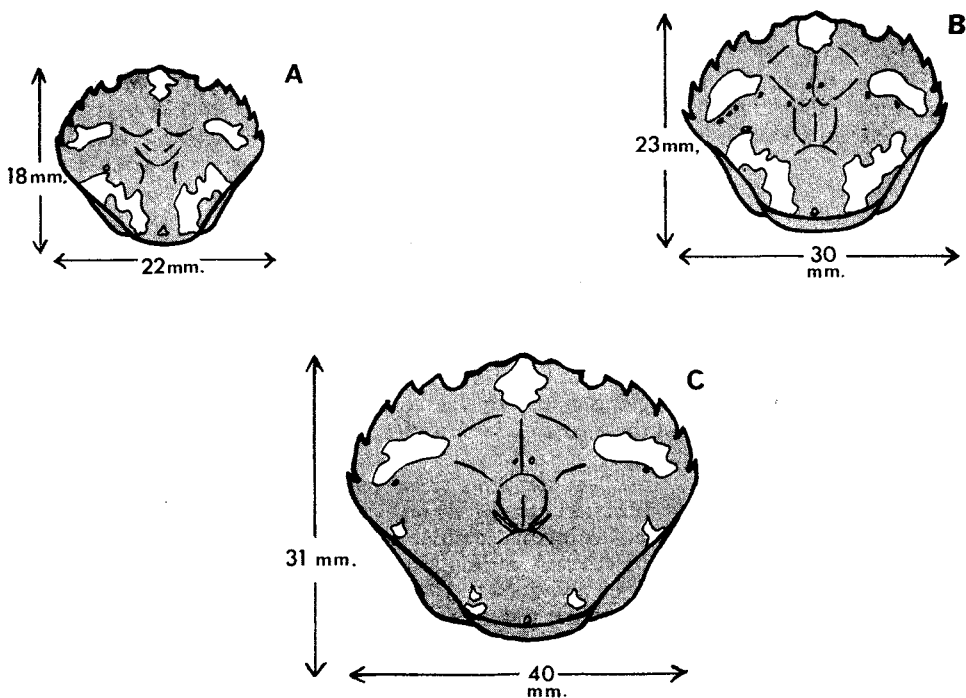


FIG. 4.

Drawings of the carapace of a young male, *C. maenas*, at three successive moults, showing alterations in shape and extent of the white patches.

representing some 3 per cent of the adult and juvenile population, are described by Provenzano (1960). In Britain symmetrical markings are more usual, but only on small crabs. Either these crabs lose the markings as they grow, or young crabs with white markings never grow up; because of disease? or parasitism?

The patches are distinctive and are more or less retained at each moult. Fig. 4 shows a young male that reached 40 mm. (in an aquarium) whilst retaining its white patches. I have been as yet unable to keep such an animal until it lost the markings, although the area seemed to be decreasing in the crab illustrated in Fig. 4. The cast skeleton turned red, except for the white areas,

which suggests either a deficiency of pigment or the presence of a substance overlying the chromoproteins. Some parasites (e.g. *Thelothania*) remove pigments from crab tissues (Perez, 1904) so it is presumably possible for a parasite to remove sufficient pigment to alter external colours. On the other hand, feeding patched crabs on a carotenoid-rich diet has yet to cause loss of the patches. Uric acid is one of the better known white pigments in crustacea, but if the patches were produced by an excretory product would they not be discarded at the moult? Yet they are present in the new integument at ecdysis. Perhaps uric acid is not an excretory product in *C. maenas*.

Rhythmical Behaviour

Many animals show behavioural cycles (=rhythms), usually associated with seasonal, day/night, or other regular phenomena (Harker, 1958, 1964). Of special importance to shore animals is the development of a tidal activity rhythm. Feeding and all other activities on the shore are largely restricted to periods of high tide and it is important that the animal should make maximum use of this period—hence the development of activity peaks in *C. maenas* at high tide (p. 594). The presence of such rhythms immediately distinguishes littoral from sub-littoral animals.

C. maenas exhibits locomotory (Naylor, 1958, 1960 and 1961; Powell, 1962*c*) and colour (Powell, 1962*a, b*) rhythms in phase with the day/night cycle, and locomotory (Naylor, 1958, 1962 and 1963; Powell, 1962*c*) and respiratory (Arudpragasam and Naylor, 1964*b*) rhythms in phase with the tides. Although in phase with external (exogenous) cycles these are internal (endogenous) rhythms and persist when the animal is kept under constant conditions, although their expression may change.

The nature of the "clock" controlling these patterns still defies complete description. It appears to function at cellular level and its nature is discussed by most of the authors referred to in this section. It must be simple in operation for, as Naylor (1958, 1960) stresses, animals with a pelagic larval stage must have a mechanism capable of being "set" to the tidal regime into which they settle and capable of compensating for the spring/neap cycle. Zoea larvae have no tidal rhythm but quickly develop a day/night rhythm when hatched in a normal environment (Hardy, 1956; Pautsch, 1961).

In the sea, environmental stimuli continually reinforce the endogenous rhythm, the cycle of light and dark via photoreceptors and the tidal cycle via thermoreceptors (Naylor, 1963). Under constant (laboratory) conditions the general form of the rhythm persists but the peaks drift away from the normal, regular cycle and individual variations appear.

CONCLUSION

The accumulated information on *C. maenas*, summarized here and in the earlier part (Crothers, 1967), points to many fields for future research. As an ecologist I feel that the lack of knowledge about relations with other species (predator/prey relationships, etc.) warrants most attention: but whatever the reader's approach this review will have served its purpose if it has posed more questions than it has answered.

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