Marine Biology 44, 337-343 (1978)

MARINE BIOLOGY

Variation in the Carapace Pattern of Juvenile *Carcinus maenas*

P.J. Hogarth

Department of Biology, University of York; Heslington, York, England

Abstract

Juvenile shore crabs (*Carcinus maenas* L.) are highly variable with respect to carapace pattern; young crabs often have conspicuous patches of white or other pigment. Adult crabs, in contrast, are drab and usually very similar in pattern. It is probable that the patterns serve to make young crabs cryptic on certain backgrounds. Juvenile crabs of carapace widths lying between 5 and 15 mm were collected from a range of British shores (totalling 48). Pattern incidence was found to relate to two factors: the percentage of weed cover (mainly of fucoids) on the shore, and the amount of mud present. Shores of high weed cover, or with much mud present, had low frequencies of conspicuously patterned crabs. The presence of patterned crabs among the juvenile population, and their absence among adults, could result from differential visual predation removing patterned crabs progressively so that only unpatterned crabs would survive to adulthood. Alternatively, individual crabs could lose their conspicuous patterns with age. Evidence is presented in support of the latter hypothesis.

Introduction

Juvenile shore crabs (*Carcinus maenas* L.) are extremely variable with respect to carapace pattern. A proportion of juvenile crabs show conspicuous carapace patterns, frequently consisting of a more or less uniform background with contrasting patches, usually in the facial and hepatic regions of the carapace. These patches may be darker or paler than the remainder of the carapace, and they are often pure white (Fig. 1). Between an unpatterned carapace and one with a particular pattern, a more or less continuous gradation of intermediate forms exists. In these the same pattern is present in varying degrees of contrast with the background of the carapace. The different patterns are, however, readily distinguishable from one another, and represent discrete morphs.

The carapace patterns of adult *Carcinus maenas* differ in detail, but resemble each other in their general drabness, and in particular by the lack of contrasting patches in the facial and hepatic regions.

Subjectively, a small crab (say <10 mm carapace breadth) often appears less conspicuous on a finely-textured background, such as fine shell gravel or sand, than a large one with an identical pattern. In natural circumstances, therefore, it may be the case that a bold pattern is cryptic when a crab is small but conspicuous when it grows.

Many visually searching predators might exploit this situation. Probably among the more important are shore fish (e.g. *Blennius* spp. and *Cottus* spp.) and birds (e.g. the herring gull *Larus argentatus* and the common sandpiper *Tringa hypoleucos*) (see Crothers, 1968).

Different frequencies of juvenile patterns are found on different shores, even within a limited area, although the relationship between shore type and pattern incidence is not a simple one. As *Carcinus maenas* has a planktonic larval stage, major genetic differences between newly settled populations of crabs within adjacent areas are unlikely. The incidence of bold patterns within an established *C. maenas* population is presumably, therefore, determined largely by factors peculiar to the shore.

In order to investigate differences between *Carcinus maenas* populations with respect to the frequency and size distri-

0025-3162/78/0044/0337/$01.40

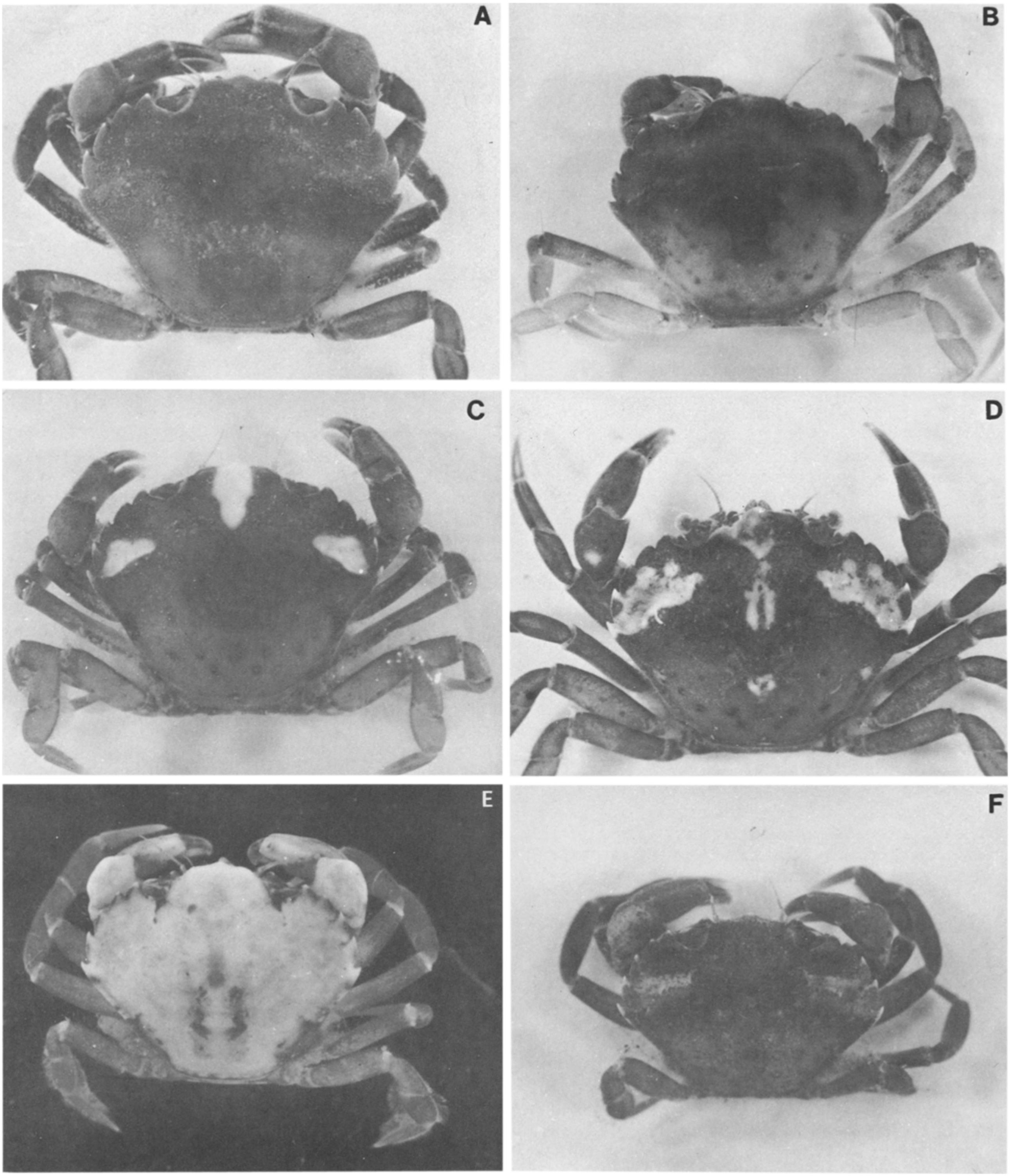

Fig. 1. *Carcinus maenas*. Carapace patterns found in juveniles. (A) uniform; (B) adult-like; (C) and (D) white (high contrast) patches in facial and hepatic regions of carapace; (E) almost uniform white; (F) low contrast patches in hepatic regions

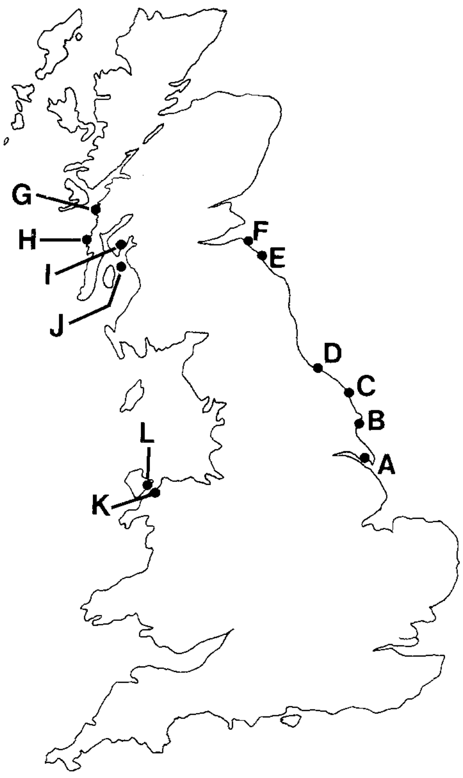

Fig. 2. Map showing locations of collecting sites. Letters correspond to those used in Table 1

bution of patterned carapaces, and if possible to relate differences between populations to shore type, populations of *C. maenas* were sampled and analysed from a total of 48 shores in the UK. Eight of these were on the Yorkshire coast, 35 on the west coast of Scotland (including 29 on the island of Greater Cumbrae), 2 on the east coast of Scotland, and 3 on the North Wales coast. The locations of the shores are shown in Fig. 2.

Materials and Methods

On each shore, the sample was taken as far as possible from within a restricted area and from the same shore level (usually within the *Fucus serratus* zone). At the time of collection, the shore was classified roughly according to substrate (sand, mud, rocks, etc.) and percentage weed cover. Within each of the major geographical areas, collecting sites were selected to represent (as far as possible) a range of shore types. In North Wales, however, all 3 sites (although they differed in other respects) were classified as muddy.

In most cases the *Carcinus maenas* were taken back live to the laboratory for analysis; where this was not possible, they were stored in 10% formalin and analysed as soon as possible after collection to minimise the effects of the loss of pigment which occurs with prolonged storage.

The breadth of the carapace of each crab was measured with dial callipers as an indication of size (Hogarth, 1975b; Klein Breteler, 1975). For each crab, facial and hepatic patterns were scored as being present or absent. If they were present, the pattern of each crab was further classified as "high contrast" (facial or hepatic patches present and white in colour) or "low contrast" (facial or hepatic patches present, but of similar shade to the rest of the carapace). "Unpatterned" crabs were those lacking facial and hepatic patches and with a carapace either uniform in colour and shade, or resembling the adult carapace in appearance.

Although juvenile *Carcinus maenas* are highly polymorphic with respect to colour as they are to pattern, the analysis which follows is based only on pattern polymorphism.

Results and Discussion

The relationship between size and pattern frequency in *Carcinus maenas* varies from sample to sample. Accordingly, in order to summarise the data for each shore, two features of the data were abstracted. Firstly, to facilitate comparisons between populations, I calculated the proportions of the three pattern categories found in crabs whose carapace breadths lay between 5 and 15 mm. These limits exclude newly-settled juvenile crabs (i.e., those not yet exposed for any significant time to whatever selection pressures operate on juveniles after settling from the plankton). Adult crabs were also excluded; the larger crabs are known to make periodic migrations between the shore and sub-littoral waters (Edwards, 1958). It was thought that the exclusion of very small and very large crabs, which are present in rapidly fluctuating numbers, would prevent bias in the comparison of different shore populations.

The second feature was the maximum size at which crabs in a particular pattern category were found. Since a single, atypically large, patterned individual could distort the estimate of maximum size at disappearance, the 5% or so of crabs with greatest carapace breadths, within each pattern category, were dis-

Table 1. *Carcinus maenas*. Frequency of high contrast carapace patterns (P_{hc}) and frequency of low contrast patterns (P_{1c}) in samples of crabs whose carapace breadths were between 5 and 15 mm. Maximum carapace breadth at which high contrast and low contrast carapace patterns were found (size at disappearance) and % weed cover at the collection site are also given. Letters in shore designations correspond with those in Fig. 2

Shore	Sample size	P_{hc}	P_{1c}	Size (mm) at disappearance hc	Size (mm) at disappearance 1c	% weed cover
A[a]	80	0.00	0.14	-	12	0
B1	57	0.16	0.38	10	10	0
B2	74	0.09	0.22	7	13	50
C1	52	0.23	0.31	12	11	0
C2	61	0.08	0.35	13	9	50
C3	36	0.28	0.19	15	19	30
C4	43	0.33	0.16	17	15	30
C5	32	0.16	0.38	15	19	30
D	30	0.19	0.38	15	13	0
E	34	0.00	0.44	4	11	90
F	49	0.20	0.22	12	26	0
G	32	0.06	0.13	16	12	-
H	55	0.24	0.54	17	13	0
I1[a]	47	0.10	0.45	14	11	100
I2[a]	55	0.14	0.55	21	20	100
I3[a]	39	0.08	0.30	5	6	0
J1	76	0.30	0.23	13	13	60
J2	75	0.07	0.46	7	13	50
J3	24	0.00	0.17	-	11	100
J4	49	0.04	0.29	13	11	60
J5	46	0.09	0.09	11	20	60
J6	49	0.16	0.39	15	22	20
J7	49	0.08	0.39	5	17	90
J8	57	0.21	0.40	14	15	1
J9	52	0.25	0.38	14	15	1
J10	86	0.13	0.27	16	18	40
J11	21	0.24	0.43	15	18	50
J12	99	0.27	0.31	13	11	20
J13	20	0.05	0.15	10	16	20
J14	110	0.29	0.36	15	20	35
J15	96	0.26	0.44	12	15	35
J16	68	0.31	0.35	21	13	0
J17	87	0.23	0.51	28	35	40
J18	85	0.11	0.37	15	24	75
J19	46	0.04	0.33	22	23	90
J20	40	0.00	0.07	35	9	80
J21	32	0.06	0.19	32	14	95
J22	66	0.08	0.45	9	14	0
J23	56	0.05	0.20	6	10	90
J24	72	0.07	0.25	17	14	40
J25	28	0.28	0.28	12	8	-
J26	39	0.15	0.23	15	14	-
J27	106	0.31	0.19	21	17	-
J28	84	0.20	0.35	17	19	-
J29	64	0.11	0.16	11	11	-
K1[a]	58	0.00	0.34	-	14	0
K2[a]	58	0.02	0.27	19	22	10
L[a]	78	0.04	0.29	10	15	30

[a] Muddy shore.

Table 2. *Carcinus maenas*. Proportions of sampled crabs whose carapace patterns were classified as high contrast, low contrast, or unpatterned. Values are expressed as means for all samples from shores of high, medium or low fucoid cover (defined as 90% or greater, between 10 and 90%, and 10% and below, respectively)

Fucoid cover	No. of shores	Proportion of crabs whose patterns were: High contrast	Low contrast	Unpatterned
High	8	0.06	0.27	0.67
Medium	19	0.15	0.31	0.55
Low	8	0.21	0.40	0.39

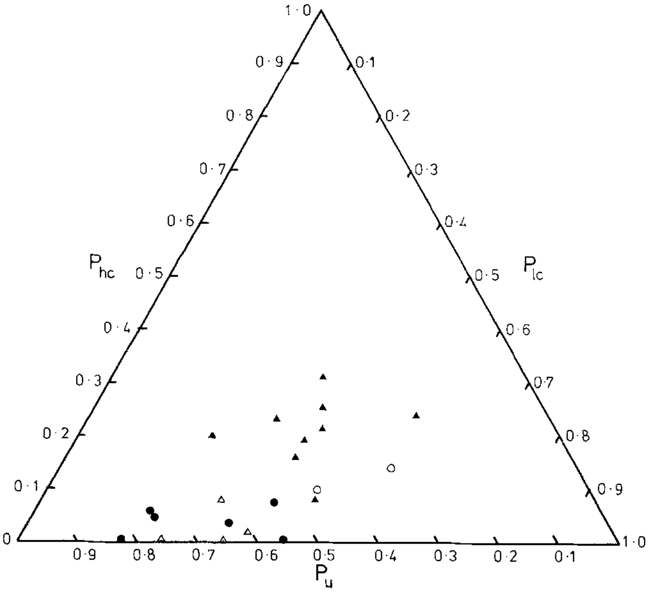

Fig. 3. *Carcinus maenas*. Observed frequencies of high contrast (P_{hc}), of low contrast (P_{1c}) and of unpatterned (P_u) crabs in shore samples. "Unpatterned" category includes adult-like patterns. Circles: shores of high fucoid cover (≥90%); triangles: shores of low cover (≤10%). For clarity, points which correspond to 27 shores of intermediate weed cover have been omitted. Open symbols refer to muddy shores, filled symbols to other shores

counted to arrive at a consistent estimate of maximum size for that category.

The results, summarised in this way, are given in Table 1.

The frequencies of the three different pattern categories, within the sampled populations of *Carcinus maenas*, are plotted in Fig. 3. It can be seen that, with the exception of the samples from the muddy shores, populations from shores of high fucoid cover differ in pattern frequencies from those obtained on shores where fucoids are sparse or absent. The former shores show lower proportions of crabs with high and low contrast patterns, and a higher proportion of crabs with unpatterned carapaces. (For 8 shores, the mean frequencies of high contrast, low contrast and unpatterned carapaces are 0.06, 0.27 and 0.67, respectively, see Table 2.) On shores of low fucoid cover, crabs with high and low contrast carapace patterns are more frequent, and those with unpatterned carapaces correspondingly scarcer (mean frequencies of 0.21, 0.40 and 0.39, respectively; mean values for 8 shores). In Fig. 3 it can be seen that the points corresponding to the samples from these two shore types fall into two distinct and virtually non-overlapping areas.

Crab populations sampled from shores with fucoid cover estimated at between 10 and 90% show a wide range of variation with respect to carapace pattern frequencies, probably due to the fact that the shores are themselves more varied than shores at either extreme of fucoid cover. Nevertheless, the mean values of pattern frequencies of these intermediate shores lie between those of high and of low weed cover. (Mean of 19 shores: high contrast, low contrast and unpatterned frequencies 0.15, 0.31 and 0.55, respectively; see Table 2.)

Samples from muddy shores appear anomalous. Of the 6 shores in question, 4 have pattern frequencies typical of shores of high fucoid cover, i.e., a relatively low proportion of high contrast patterns and a high proportion of unpatterned and low contrast crabs. Samples from the remaining two muddy shores show a higher proportion of crabs with low contrast patterns and a lower proportion of unpatterned crabs, which is similar to the composition of populations on shores of low fucoid cover. These two shores were atypical in several respects, being near the extremity of a fjord-like and very sheltered sea loch. The exposure would therefore be very low, and despite the muddy nature of the shore the water is probably seldom highly turbid. In this respect, they may differ from the other muddy shores, all of which were exposed to considerable wave action. Possibly constantly turbid water, like high fucoid cover, results in a population of juvenile *Carcinus maenas* with very low frequencies of highly contrasting carapace patterns; the common factor in the two situations may be reduction in incident light falling on the crabs.

The results in Table 1 do not indicate that variation in the composition of different samples with respect to pattern frequency is attributable to geographical area. There is no evidence of clinal variation in pattern frequency.

Two general hypotheses might explain the differences in carapace frequencies found on different shores, and the tendency of juvenile patterns to disappear from a population with increasing age. Firstly, in individual crabs, the pattern may be lost, or masked by increased pigment deposition in the carapace. Different environmental circumstances might cause acceleration, retardation or even reversal of the process of loss or masking of a carapace pattern. The similarity between populations from areas of high fucoid cover and those from constantly turbid waters on muddy shores suggests that the level of incident light reaching a crab might possibly be one relevant environmental factor. Differences between the substrate of different shores might therefore result in differences in frequencies of carapace patterns between populations, with local heterogeneity perhaps determining the variety of patterns within a population. Secondly, selective visual predation might preferentially remove from the population crabs with conspicuous patterns, resulting in an increase, with age, of the proportion of crabs with inconspicuous patterns. All adult crabs are inconspicuously patterned, but a high proportion of each successive generation of young crabs is patterned. This suggests that during development the transition from a juvenile to the adult phenotype is made by individual crabs. Differential visual predation might affect the time of transition from juvenile to adult pattern as well as the frequency within the population of innately patterned crabs. In an environment where a bold pattern became increasingly conspicuous with increasing size, selection would favour an earlier transition.

This mechanism would not, of course, preclude the possibility that on some backgrounds selection by visual predation might favour patterned crabs at the expense of unpatterned. This could apply only to small crabs, as patterned carapaces are consistently rare among crabs over 25 mm breadth.

A further consideration is that all crabs might not be equally exposed to predators. Crabs of different ages probably differ behaviourally, for example in the proportion of time spent searching for food or for a place in which to moult. They would therefore differ also in the duration of their exposure to the risk of predation. Large crabs may rely for survival on active defence, rather

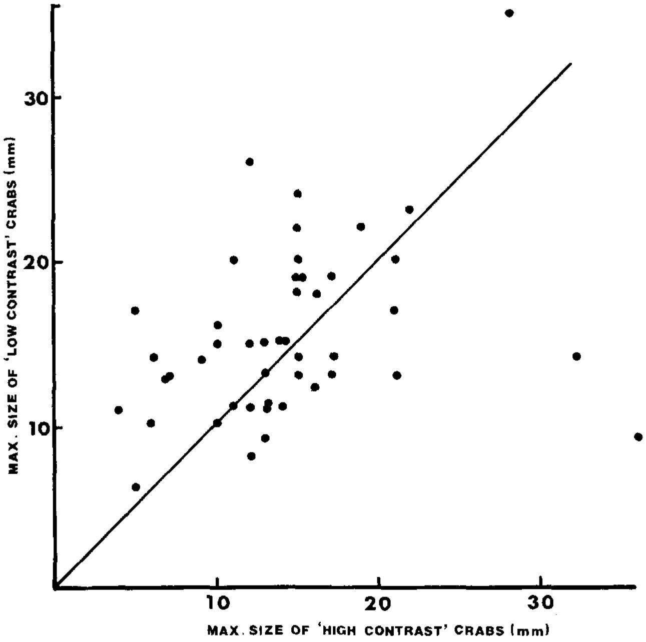

Fig. 4. *Carcinus maenas*. Carapace breadths above which crabs in a particular pattern category were absent from samples (discounting the largest 5% of patterned ones in each sample)

than on crypsis. (Although observation of the feeding behaviour of larid gulls, and analysis of the crab remains which litter rocks where gulls habitually roost, suggest that this is less than totally effective.)

If selection by visual predation acted to remove, differentially, conspicuously patterned crabs from the population, then more conspicuous patterns would be expected to disappear from the population earlier than less conspicuous ones. The frequency of highly conspicuous patterns would decline with increasing size (that is, with increasing age) more rapidly than that of less conspicuous patterns. The sample collections were analysed to see whether this was in fact the case.

Fig. 4 compares the size at which high and low contrast patterns disappear from the population. The relation between the two indicates that, in samples from 44 populations, there is no tendency for high contrast juvenile patterns to disappear from the population at a smaller size than low contrast juveniles. (A brief preliminary account of this aspect of the present study has already been published: Hogarth, 1975a.)

If selective visual predation were of primary importance in determining the size distribution within the population of high and low contrast juvenile patterns, it would be predicted that the more conspicuous high contrast patterns would disappear sooner from the population; i.e., at a smaller mean size. This does not appear to be the case. Consequently, it can be concluded that some other mechanisms are probably of greater importance in determining the rate of disappearance, with age, of patterned crabs.

If selective visual predation is not of direct importance in determining the observed pattern frequencies of *Carcinus maenas*, it seems probable that individual juveniles have the ability to modulate or lose totally their carapace patterns. This is also suggested circumstantially by the fact that patterns are exceedingly rare in sexually mature adult crabs, but common in each successive generation of young crabs.

Very young crabs (up to about 5 mm carapace breadth) can alter the colour and shade of their carapace to match varied backgrounds by expansion and contraction of chromatophores (Crothers, 1968); no evidence has been published of their ability to alter carapace pattern in this way. Powell (1962) describes the loss, with age, of a striped pattern from the legs of juvenile *Carcinus maenas* (specifically on the merus of the last pereiopod), and related the rate of loss to the nature of the substrate. However, it is not possible to infer from Powell's results how much of the change of pattern occurred within an instar, and how much at ecdysis.

Older crabs lose flexibility in colour and pattern changes. Due to the opacity of the carapace, any significant changes in colour or pattern can occur only at ecdysis. Crothers (1968) found little sign of pattern changes actually occurring at ecdysis; however, he describes the carapace patterns of only three successive instars of a single crab.

The question of phenotypic plasticity of carapace pattern in response to environmental circumstances is currently being investigated. Preliminary results, with juvenile crabs of premoult carapace breadths between 10 and 30 mm, indicate that patterns are, in general, stable at ecdysis. In approximately 30% of cases, minor changes are detectable following a moult; in 10% of cases, striking alterations in the pattern may occur, usually in the form of expansion or contraction of pattern elements already present. In some cases, pattern elements disappear altogether or (rarely) may develop where they were not apparent before. Loss or gain of pattern elements does not, of course, preclude some genetic specification of the potential pattern repertoires of individual crabs.

The size incidence of patterned crabs within a population and the differences in incidence between populations are, therefore, probably the result primarily of the physiological responses of individual crabs to their immediate background.

Acknowledgements. I should like to thank J.G. James for his help with collecting and photographing the crabs, and Drs. M. Carter and G.S. Oxford for their helpful criticism of the manuscript of this paper.

Literature Cited

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

Edwards, R.L.: Movements of individual members in a population of the shore crab, *Carcinus maenas* (L.) in the littoral zone. J. Anim. Ecol. *27*, 37-45 (1958)

Hogarth, P.J.: Pattern polymorphism and predation in the shore crab, *Carcinus maenas* (L.). Crustaceana *28*, 316-319 (1975a)

\- Instar number and growth of juvenile *Carcinus maenas* (L.). Crustaceana *29*, 299-300 (1975b)

Klein Breteler, W.C.M.: Growth and moulting of juvenile shore crabs, *Carcinus maenas*, in a natural population. Neth. J. Sea Res. *9*, 68-99 (1975)

Powell, B.L.: Types, distribution and rhythmical behaviour of the chromatophores of juvenile *Carcinus maenas* (L.) J. Anim. Ecol. *31*, 251-261 (1962)

Dr. P.J. Hogarth
Department of Biology
University of York
Heslington
York YO1 5DD
UK

Date of final manuscript acceptance: August 19, 1977. Communicated by J.H.S. Blaxter, Oban