



## CHELA DIMORPHISM AND HANDEDNESS IN THE SHORE CRAB *CARCINUS MAENAS*

H. J. PYNN

Department of Zoology, Oxford University.

### ABSTRACT

*Carcinus maenas* is heterochelous and shows strong evidence of handedness with crusher chelae being found predominantly on the right and cutters on the left side of undamaged crabs. If the right crusher chela is lost, the cutter on the left changes into the new crusher. This phenomenon, known as reverse handedness, is seen more often in males or older crabs. Studies of the gaps between the propus and dactylus reinforce the data for heterochely as cutters have no (or only small) gaps whereas crushers, especially in males, have large and sometimes exaggerated gaps. A regenerated chela will grow to the same size as the one it has replaced. Further work is required to test whether the regenerates are as physically capable as the original chelae.

### INTRODUCTION

Crab appendages are segmentally arranged, with one pair on each embryonic segment (see Crothers, 1967). The most anterior pair of thoracic limbs, the claws, have evolved into appendages that are very different to the walking legs and are enlarged, chelate and used both in feeding and fighting (Mearow & Govind, 1986).

A prominent feature of many shore crabs, *Carcinus maenas* (L.), is the bilateral asymmetry due to morphologically dissimilar chelae (Fig. 1). Crustacea showing this condition are termed 'heterochelous' (Elner, 1978). The major (crusher) chela is larger, more robust, and has enlarged molar-like dentition. It serves to crush prey using its greater mechanical advantage (Warner, Chapman, Hawkey & Waring, 1982). The cutter is more slender, has incisor-like teeth on its biting surface and serves to manipulate the prey using finer and more co-ordinated movements. Heterochely is less marked in female shore crabs where both chelae are 'cutter-like'.

The heterochely has been related to feeding technique. When feeding on a mussel, for example, the shell must be broken open and the flesh then extracted through a narrow opening (Elner, 1978). However, *C. maenas* does not always possess both crusher and cutter chelae. It is relatively common for a crab to be missing one of its chelae (personal observation). These may have been cast off to enable the crab to escape from a predator, or to release itself when trapped by a displaced rock and will be regenerated at the next moult (see Crothers, 1967). The appendage is shed at a designated pre-formed breakage plane, near the base of the limb. Strangely, this part of the limb is not the weakest but one where damage to the stump is minimal and where a double membrane ensures that the stump is immediately sealed off from the exterior as soon as the limb is lost to prevent bleeding and infection (see Crothers, 1968; McVean, 1972).

Swartz (1972) looked at 1601 specimens of the Caribbean mud crab, *Neopanope sayi*, and found that 79.9% had a right crusher and left cutter, 12.6% had the opposite configuration, 3.4% had two cutters and 4.0% were missing one or both chelae. However, heterochely

does not always show the same handedness. In lobsters, *Homarus gammarus*, the distribution of right and left handedness is equal - i.e. 50% right : 50% left (Przibram, 1931). Furthermore, this ratio is not altered by regeneration and a cutter replaces a cutter. Whatever the handedness, in all heterochelous Crustacea, the asymmetry of the chelae increased as they grew larger (Przibram, 1931).

Studies of the American blue crab, *Callinectes sapidus*, by Hamilton, Nishimoto & Halusky (1976) showed that the frequency of crabs with right crushers and left cutters decreased as the carapace length increased and, conversely, the frequency of crabs with left crushers and right cutters increased. This phenomenon (left crusher and right cutter) is known as 'reverse handedness' (Hamilton *et al.*, 1976). It only occurs after a crab has lost its original master chela. Hamilton *et al.* found that all their crabs regenerating a right chela were growing a cutter and that the surviving cutter on the left side had changed into a crusher. Govind & Blundon (1985), also working with *C. sapidus*, found that the mechanical advantage of a newly-converted crusher, although greater than that of the regenerated cutter, was less than that of the original crusher due to the retention of the cutter-type closer muscle.

A great deal of stress is put on the importance of the crusher chela in the literature but few or no crabs have two crushers. Thus, the cutter must be equally important. Heterochely does not always happen (Hamilton *et al.*, 1976). Some crabs have two cutters (especially females and very large males). Przibram (1931) found that the carapace width of crabs with two cutters was significantly ( $p < 0.01$ ) greater than that of crabs with dimorphic chelae. He suggested that a large cutter could produce enough force for most crushing tasks and so there would be no benefit in these crabs expending additional energy in growing a crusher.

Nobody has demonstrated differences in the food preferences of male and female crabs, so the form of male chelae may be influenced more by mating than feeding behaviour. This implies that a crusher is mainly used for intimidatory purposes. The male with the wider chela-span is superior (Berrill & Arsenault, 1982). Chelae are often lost by males during fighting, especially in the mating season which occurs from July to September in Milford Haven - it varies between locations (Crothers, 1967). It has been suggested that females are less aggressive, do not have to compete for mates and so have less need for a crusher.

The aims of the present work were:

- (1) To investigate heterochely in *Carcinus maenas* to establish whether the crusher chela predominately lay on the left or right side of the crab - or whether there was no preference.
- (2) To compare regenerated chelae with the ones that they had replaced.

#### MATERIALS AND METHODS

One hundred and twenty four male, and one hundred and nine female, *C. maenas* were collected from low intertidal rocky shores and shallow subtidal habitats of the Milford Haven region of Pembrokeshire, South Wales, between April and July 1995 in two locations - Freshwater West Bay and the Jolly Sailor Pier at Burton in Milford Haven. Most were collected at the Jolly Sailor Pier using a drop-net baited with bacon bits. The crabs were removed from the net carefully to avoid any loss of limbs in the process and placed in buckets of sea water to await measurement.

Measurements 1-5 (below) of body and limbs were made to the nearest 0.5 mm with Vernier callipers (see Fig. 1)

- (1) Carapace length, determined as the distance between the two most lateral carapace spines.
- (2) Carapace width, determined as the distance between the edge of the carapace midway between the eyes to the first abdominal segment.
- (3) Length of leg 3; the distance from the coxopodite to the tip of the straightened limb.

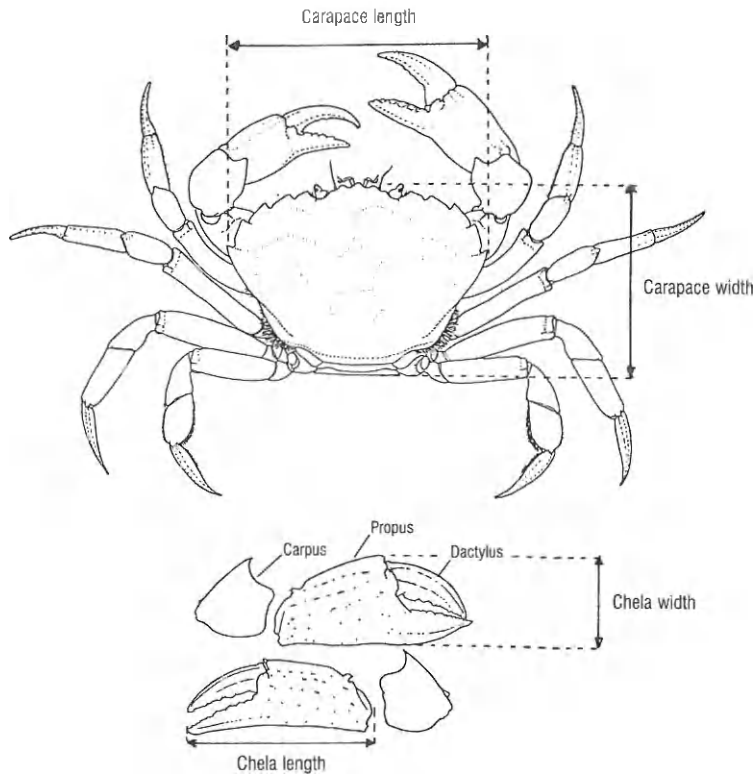


FIG. 1. *Carcinus maenas*, showing the dimensions measured and the asymmetry of chelae in a male. Note the difference in tooth size between the chelae. The gap is measured at its widest point when the chela is in the closed state. Drawings by Marilyn Crothers from Crothers & Crothers (1983) and Crothers (1967).

- (4) Length of left and right chelae, determined as the distance from the carpus-propus joint to the tip of the propus along the ventral surface.
- (5) Width of the left and right chelae, determined as the widest distance between the top and bottom of the propus.

Designating a chela as 'crusher' or 'cutter' might be a subjective assessment. To obtain an objective measurement of chela type, the gap between the propus and dactylus of each chela (determined as the widest gap remaining when the pincers were closed) was measured, to the nearest 0.1 mm, using a feeler gauge. However, as chela gaps could not be measured to a greater accuracy than 0.1 mm, all chelae with no apparent gap were recorded as having a gap of 0.0 mm. A chela was described as a crusher if it had a gap of more than 0.1 mm. Crushers have large gaps to hold the prey whereas the cutters have no or very small gaps (Przibram, 1931).

The crabs were sexed following using the following characters (Crothers, 1967):

- (a) shape of the abdomen; pointed in males and rounded in females.
- (b) apparent number of segments on the abdomen; males have 5, females have 7.
- (c) presence of setae; the adult female has setae around the edge of the abdomen. The male has no such setae.

After measurement, the crabs were marked before being released to avoid the same crab being measured twice.

## RESULTS

The data presented in the Tables show a very significant trend for handedness in *Carcinus maenas*. Typically, the crabs showed a crusher on their right side and a cutter on their left, although 32 out of the 211 specimens with both chelae intact showed no apparent handedness and 22 others had one or both chelae missing.

Figs 4-7 display the data on the gaps between the propus and dactylus (see Fig. 1).

TABLE 1. *The degree of handedness in Pembrokeshire Carcinus maenas*

Serial	Crab description	Number	%
1	Total number of crabs	233	
2	With missing chela(e)	22	
3	Crabs in test	211	
4	With right crusher	156	74
5	With left crusher	23	11
6	No apparent handedness	32	15
7	Expected value for (6)	105.5	50

A chi-squared test for right handedness gave

$$\chi^2 = 24.17 \text{ with one degree of freedom; } p < 0.0001 - t_{(crit)} = 15.14.$$

TABLE 2. *Handedness in female C. maenas.*

Serial	Female crab description	Number
1	Number of female crabs	109
2	Number with no apparent crusher	15
3	Number with right crusher	76
4	Number with left crusher	9
5	Number with missing chelae	9

A chi-squared test for right handedness gave

$$\chi^2 = 13.52 \text{ with one degree of freedom; } p < 0.001 - t_{(crit)} = 10.83.$$

TABLE 3. *The percentage of males and females showing reverse handedness.*

Serial	Crab description	males		females	
		n	%	n	%
1	Crabs in sample	124		109	
2	Crabs showing reverse handedness	14	11.3	9	8.25
3	Crabs missing chela(e)	13	10.5	9	8.25
4	Total crabs showing variation from 'normal'	27	21.8	18	16.5

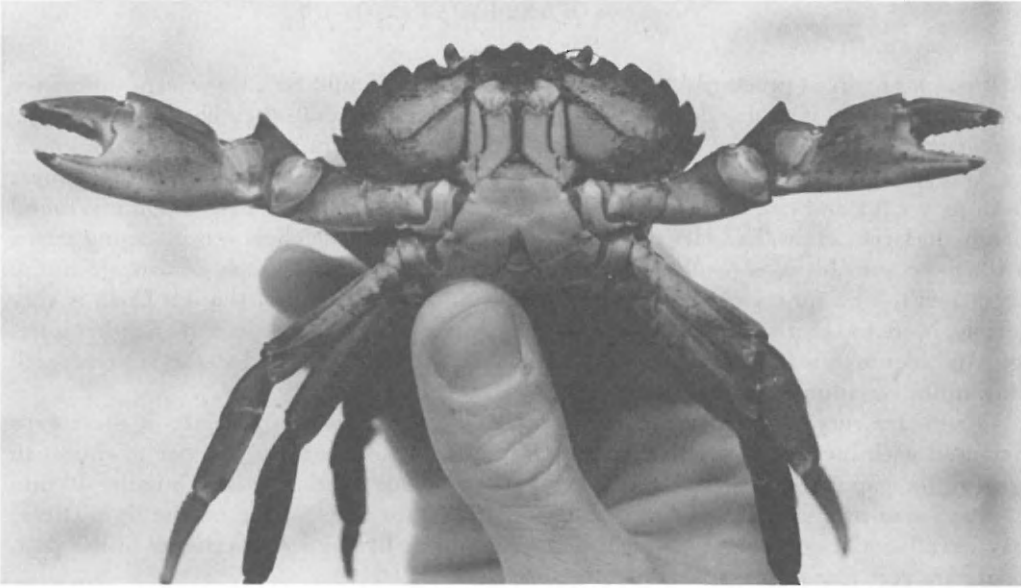


FIG. 2 Male *Carcinus maenas*, showing the triangular abdomen without a fringe of setae. On the left (the crab's right) is a crusher chela and on the right (the crab's left), a cutter chela. Photograph by Dr H. C. Bennet-Clark

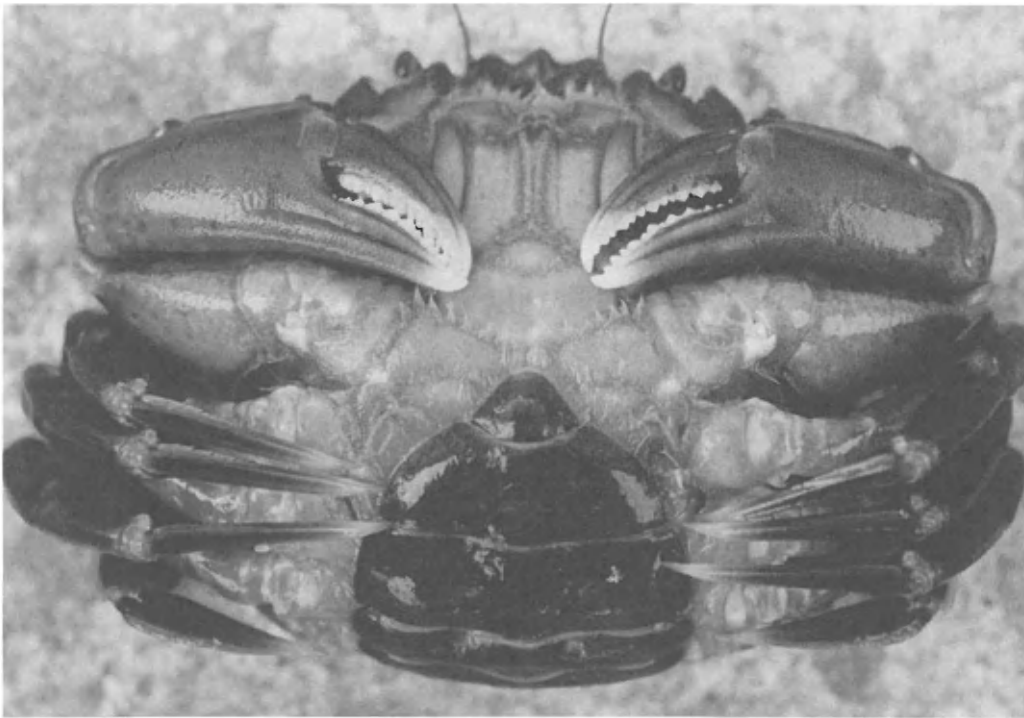


FIG. 3 Female *Carcinus maenas* showing the rounded abdomen fringed by setae and the two cutter-type chelae. Photograph by Dr H. C. Bennet-Clark

## ANALYSIS OF THE DATA IN FIGS 4-8

*Handedness*

If *C. maenas* really is predominately right handed, there should be a significant difference between the gaps of chelae depending on which side of the crab they lie - crushers have large gaps to hold the prey whereas the cutters have very small or no gaps (Przibram, 1931).

Many left chelae had little or no gap between the propus and dactylus (many datapoints lie along  $y = 0.1$  and  $y = 0.01$ ) and were, by definition, cutters (Figs 4 and 5). Others, found mainly on larger crabs, had large gaps which indicated that the chela was changing into a crusher (presumably as a result of right chela regeneration) or because of damage to the larger teeth. The spread of the data shows that the morphology of the left chela is very flexible. Note too that variation in left chelae increased with carapace length and, therefore, age. An older crab is more likely to have had its chela(e) damaged and so the left chela will show more variation to compensate for loss of right chelae (Berrill, 1982).

There are very few right chelae with no gaps (Figs 6 and 7). The size of these gaps increased with increased carapace length, giving regression lines of steeper gradient. In general, the gap increased from under 1 mm in crabs with a carapace length under 40 mm to over 5 mm in individuals only twice as big. The crabs with no gap on the right chelae may have been re-growing a chela in the cutter form, having lost a crusher in the past. There are very few such crabs with cutter-like right chelae.

*Differences between the sexes:*

Heterochely is most pronounced in males. The largest gap in a female chela was only 2.1 mm compared to a male's 5.1 mm. It seems that a significant number of females do not have a gap in either of their chelae. But a chi-squared test on the female data (Table 2) showed that crushers were still evident in females.

*Regenerated chelae.*

Przibram (1931) stated that 'it is the claw that is not lost that always develops into the crusher'. This is one of the assumptions of this analysis, the other being that handedness must be in evidence. The aim was to compare the size of the lost chela with that of the new chela (i.e. when a right crusher is lost, how did it compare with the converted left chela that replaced it).

There are two possible methods for investigating this:

- (1) From the plot of chela length/width against carapace length (Figs 8A and 8B). The drawback is that this assumes that the particular crab followed the correlation but if the value of  $R^2$  is high then this is a reasonable assumption.
- (2) Looking at the size of the converted left chela. However, it is not clear if it has finished growing.

The analysis used male crabs as they show more evidence of dimorphism in their chelae (Govind, 1985) and were expected to show an increased frequency of reversed handedness (Table 3). However, the data did not allow me to reject the null hypothesis at the 5% level. A 2 x 2 contingency table gave.

$$\chi^2 = 0.720 \text{ with one degree of freedom; } p > 0.05 - t_{(crit)} = 3.84.$$

In Fig. 8A, for right-handed male crabs, the regression lines fit the data well, giving high values of  $R^2$ . Fig. 8B, which is the more interesting in terms of regeneration capability, shows the same regression lines with data for left-handed male crabs superimposed. Although there are only 16 left-handed crabs, it is quite clear that their left chelae had developed into the form of the original right chelae. The points for right chelae are more variable due to the various stages of regeneration. However, in older crabs, it appears that complete role reversal of the chelae has been undertaken. It seems that reverse handedness is more likely to be seen in larger crabs as not only have they lived longer and are more likely to have lost a right chela but also that the new chela is more likely to have finished growing (i.e. fully differentiated reverse handedness).

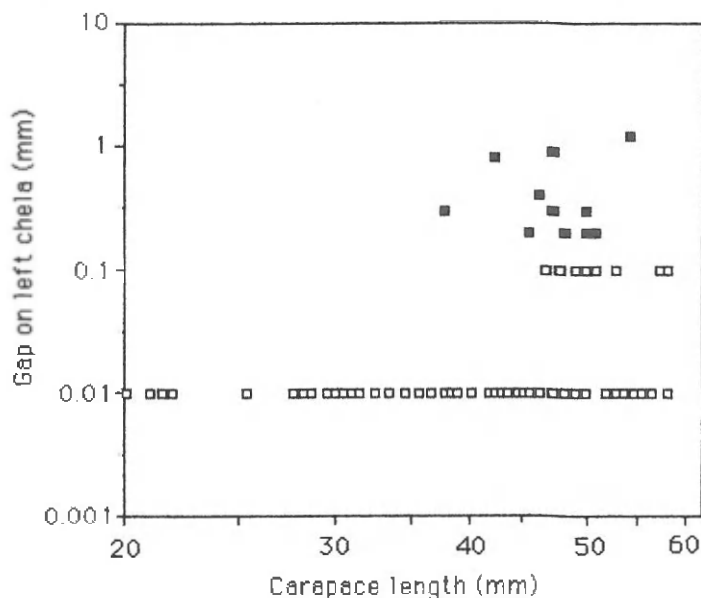


FIG. 4. The relationship between left chela gap and carapace length in female *Carcinus maenas*, plotted on logarithmic scales. Chela gaps could not be measured to an accuracy greater than 0.1 mm, hence the cluster of points along the line  $y = 0.1$ . All chelae with no apparent gap were given a gap of 0.01 mm, hence the cluster along  $y = 0.01$  mm.

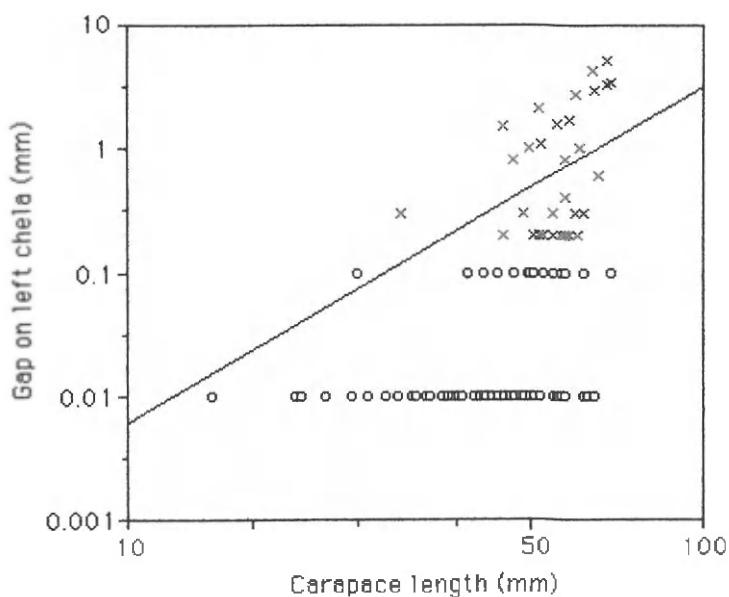


FIG. 5. The relationship between left chela gap and carapace length in male *Carcinus maenas*, plotted on logarithmic scales.  $R^2$  for chelae  $> 0.1$  mm = 0.248. Chela gaps could not be measured to an accuracy greater than 0.1 mm, hence the cluster of points along the line  $y = 0.1$ . All chelae with no apparent gap were given a gap of 0.01 mm, hence the cluster along  $y = 0.01$  mm.

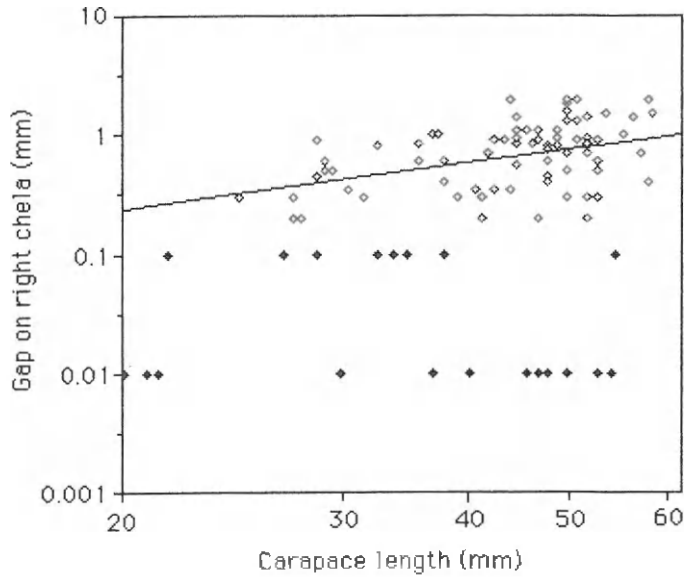


FIG. 6. The relationship between right chela gap and carapace length in female *Carcinus maenas*, plotted on logarithmic scales.  $R^2$  for chelae  $> 0.1$  mm = 0.261. Chela gaps could not be measured to an accuracy greater than 0.1 mm, hence the cluster of points along the line  $y = 0.1$ . All chelae with no apparent gap were given a gap of 0.01 mm, hence the cluster along  $y = 0.01$  mm.

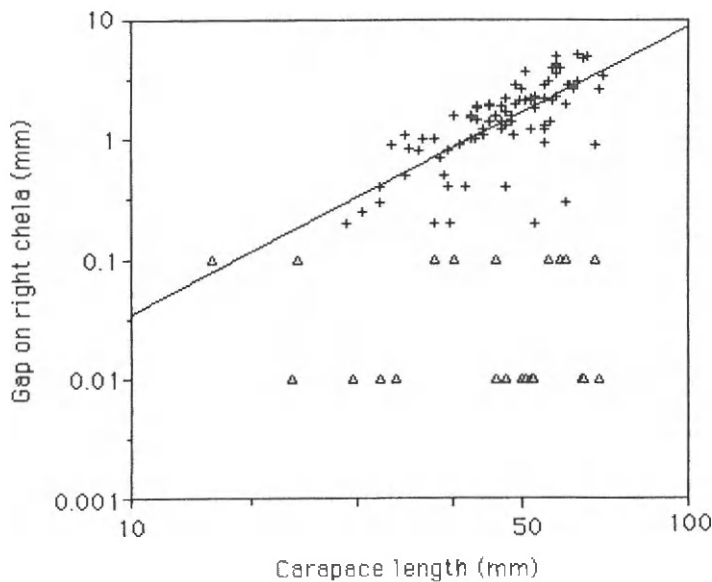


FIG. 7. The relationship between right chela gap and carapace length in male *Carcinus maenas*, plotted on logarithmic scales.  $R^2$  for chelae  $> 0.1$  mm = 0.502. Chela gaps could not be measured to an accuracy greater than 0.1 mm, hence the cluster of points along the line  $y = 0.1$ . All chelae with no apparent gap were given a gap of 0.01 mm, hence the cluster along  $y = 0.01$  mm.



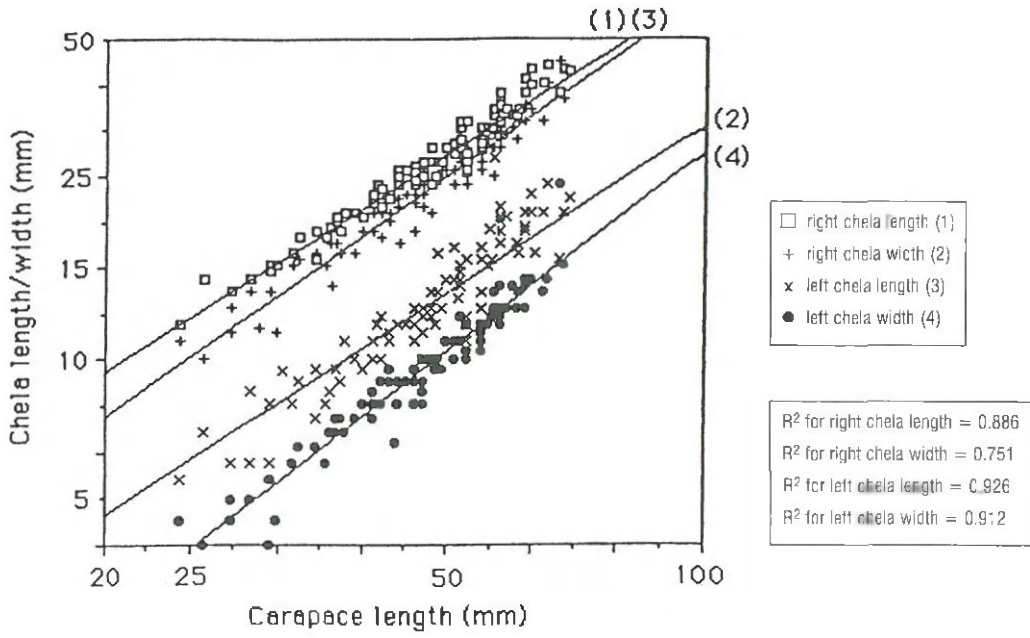


FIG. 8A. The relationship between chela length or width and carapace length in male right-handed *Carcinus maenas*, plotted on logarithmic scales.

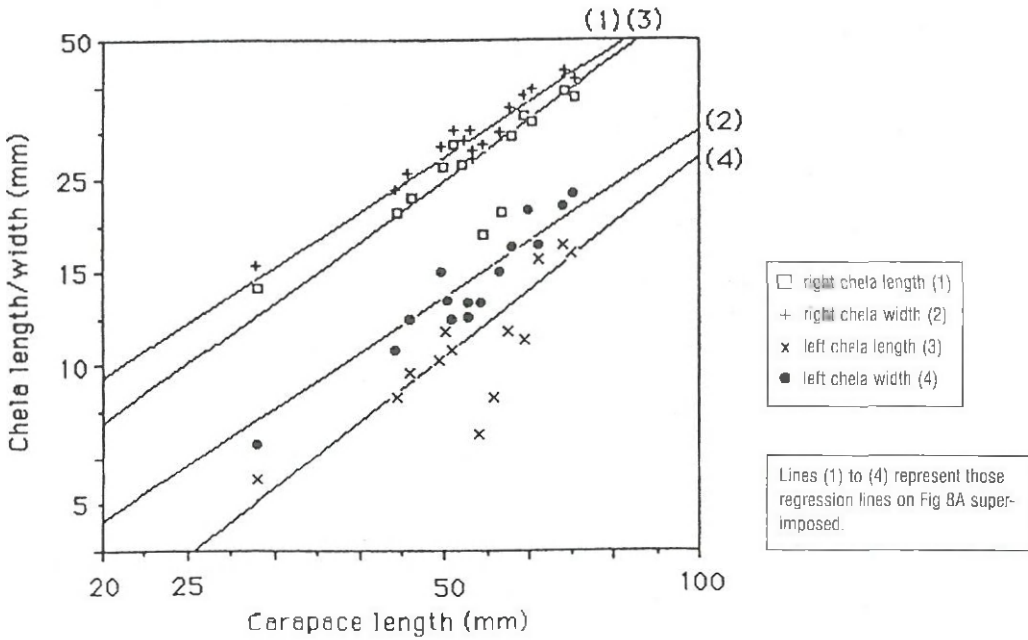


FIG. 8B. The relationship between chela length or width and carapace length in male LEFT-handed *Carcinus maenas*, plotted on logarithmic scales. The points have been superimposed on the regression lines derived from right-handed crabs in Fig. 8A.

The aim was to see if the crusher chela forming on the left hand side was as large as the one it has replaced. From Fig. 8B, it seems that the regenerated chela does grow to a similar size as the datapoints from right and left sides fully reverse but follow the original regression lines. But, do they have the same muscular capacity?

#### DISCUSSION

The analysis of these data suggests that the shore crab, *C. maenas*, does show chela dimorphism (heterochely) in both males and females - as do many other species of Crustacea (Przibram, 1931, Govind *et al.*, 1978, Attrill *et al.*, 1991). Moreover, *C. maenas* shows right handedness.

Przibram (1931) hinted at the possibility of handedness in many species of Crustacea although no quantitative analysis was produced. Yamaguchi (1977) studied heterochely in fiddler crabs (*Uca lactea*) and found that the males showed exaggerated dimorphism of the chelae (the large chela develops rapidly at sexual maturation) whereas the females have two small, equally-sized chelae. However, *U. lactea* showed no specific handedness - which side bore the crusher occurred by chance or was determined by the loss of the other chela. One purpose of this paper was to obtain evidence for handedness in *C. maenas*.

The analysis of the data in Table 1 showed a high degree of right-handedness of the crusher chela. The dimorphism was greater in males than in females, presumably because chelae are the primary implements used in aggressive display and conflict (Berrill & Arsenault 1982) and this is a major activity of males. Selection should favour males with larger chelae. But the present evidence suggests that the cutter may be the more important because there are no occurrences of a crab with two crushers yet there were several members of the sample with two cutters.

Hamilton *et al* (1976) found the incidence of crabs with two cutters was greater in larger crabs where the cutter was able to produce enough force for most crushing tasks, thus making dimorphism unnecessary. The present data do not support this hypothesis, probably because *C. maenas* does not grow to a size large enough to have cutters capable of producing sufficiently high forces. It would be interesting to study how the crab reacts if the cutter is removed.

Handedness was also investigated by studying the gaps between the propus and dactylus of the chelae. Guchardi & Govind (1989) stated that the chelae of *C. maenas* were largely identical in external morphology and function and only differed in size. However, the present data shows that the gaps of left and right chelae differed greatly. Variation in the size and presence of gaps can be explained if regeneration leads to reverse handedness.

Where reverse handedness occurs, the chelae appear to be similar in size to normally-handed chelae suggesting that the regenerated chelae grow to the same size as the original chela. Govind (1985) found that the crusher chelae of blue crabs with reverse handedness were not able to exert greater forces than the cutters. When he compared similarly sized right and left crushers from two different crabs, left crushers were weaker and had a smaller mechanical advantage. Govind concluded that the muscle of the regenerated chela is not crusher muscle (i.e. the muscle had remained cutter muscle). It would be interesting to compare the muscle anatomy of normally-handed chelae with those showing reverse handedness.

Hartnoll (1982) stated that heterochely was common among the Crustacea but that distinct handedness was comparatively uncommon, with most crab species being equally likely to have the left or right chela as the crusher. *C. maenas* seems, therefore, to be unusual with its very significant trend for having the crusher on the right.

#### ACKNOWLEDGEMENT

I am indebted to Dr H. C. Bennet-Clark of this department for providing the photographs reproduced as Figs 1 and 2 as well as ideas and constructive criticism throughout the preparation of this material.

## REFERENCES

- ATTRILL, M. J., HARTNOLL, R. G. and RICE, A. L., (1991). Aspects of the biology of the deep-sea crab *Geryon trispinosus* from the Porcupine seabight. *Journal of the Marine Biological Association, U.K.*, **71**, 311-328.
- BERRILL, M., and ARSENAULT, M., (1982). Mating behaviour of the green shore crab *Carcinus maenas*. *Bulletin of marine science*, **32**, 632-638.
- CROTHERS, J. H., (1967). The biology of the shore crab, *Carcinus maenas* (L.). 1 The background - anatomy, growth and life history. *Field Studies*, **2**, 407-434.
- 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.
- CROTHERS, JOHN and CROTHERS, MARILYN, (1988). A key to the crabs and crab-like animals of British inshore waters. *Field Studies*, **5**, 753-806.
- EDWARDS, R. L., (1958). Movements of the individual members in a population of the shore crab *Carcinus maenas* (L.) in the littoral zone. *Journal of Animal Ecology*, **27**, 37-45.
- ELNER, R. W., (1978). The mechanics of predation by the shore crab *Carcinus maenas* (L.) on the edible mussel, *Mytilus edulis* (L.). *Oecologia*, **36**, 333-344.
- GOVIND, C. K. and LANG, F., (1978). Development of the dimorphic claw closer muscles of the lobster *Homarus americanus*. III. Transformation to dimorphic muscles in juveniles. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole*, **154**, 55-67.
- GOVIND, C. K. and BLUNDON, J. A., (1985). Form & function of the asymmetric chelae in blue crabs with normal & reversed handedness. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole*, **168**, 321-331.
- GUCHARDI, J. A., and GOVIND, C. K., (1989). Vascular supply to bilaterally asymmetric chelae in crustaceans. *Canadian Journal of Zoology*, **68**, 1062-1064.
- HAMILTON, P. V., NISHIMOTO, R. T., and HALUSKY, J. G., (1976). Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). *Biological Bulletin of the Marine Biology Laboratory, Woods Hole*, **150**, 393-401.
- HARTNOLL, R. G., (1982). *Growth*. In *The Biology of the Crustacea*, Vol. 2. Embryology, Morphology & Genetics, (ed. L. G. Abele). New York - Academic Press.
- INGLE, R. W., (1980). *British Crabs*. Oxford University Press.
- MCVEAN, A. R., (1972). Autotomy in *Carcinus maenas* (Decapoda: Crustacea). *Journal of Zoology, London*, **169**, 349-364.
- MEAROW, K. M. and GOVIND, C. K., (1986). Neuromuscular properties in serially homologous lobster limbs. *Journal of Experimental Zoology*, **239**, 197-205.
- PRZIBRAM, H., (1931). *Connecting laws in animal morphology*. University of London Press.
- SCHMIDT-NIELSEN, K., (1984). *Scaling-Why is animal size so important?* Cambridge University Press.
- SWARTZ, R. C., (1972). *Postlarval growth and reproduction in the xanthid crab, Neopanope taxanasi*. Doctoral dissertation, College of William & Mary.
- VERMEIJ, G. J., (1977). Patterns in crab claw size: the geography of crushing. *Systematic Zoology*, **26**, 138-151.
- VERNBERG, F. J. and COSTLOW, J. D. Jnr., (1966). Handedness in fiddler crabs, (genus *Uca*). *Crustaceana*, **11**, 61-64.
- WARNER, G. F. and JONES, A. R., (1976). Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology, London*, **180**, 57-68.
- WARNER, G. F., (1977). *The Biology of Crabs*. Elek.
- WARNER, G. F., CHAPMAN, D., HAWKEY, N. and WARING, D. G., (1982). Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). *Journal of Zoology, London*, **196**, 431-438.
- WEIS, J. S., (1976). Effects of environmental factors on regeneration and moulting in fiddler crabs. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole*, **150**, 152-162.
- YAMAGUCHI, T., (1973). Asymmetry and dimorphism of chelipeds in the fiddler crab, *Uca lactea*. *Zoological Magazine*, **82**, 154-158.
- YAMAGUCHI, T., (1977). Studies on the handedness of the fiddler crab, *Uca lactea*. *Biological Bulletin of the Marine Biology Laboratory, Woods Hole*, **152**, 424-436.

