

## ADDUCTION LEVERS AND ADDUCTOR MUSCLE FUNCTION IN THE MANDIBULAR SYSTEM OF THE SHORE CRAB *CARCINUS MAENAS*

BY N. J. ABBY-KALIO\* AND G. F. WARNER

*Department of Pure and Applied Zoology, University of Reading, Whiteknights,  
PO Box 228, Reading, RG6 2AJ, UK*

*Accepted 9 May 1986*

### SUMMARY

The lever systems, and structure and function of the adductor muscles, of the mandibles of large male *Carcinus maenas* (L.) were investigated. The functional mechanical advantage (FMA) of the external adductor muscles, measured at the middle of the biting edge of the mandible, was  $1.53 \pm 0.01$ ; the ideal mechanical advantage (IMA), calculated from measured lever lengths, was  $1.78 \pm 0.03$  (mean  $\pm$  s.e.). The FMA of the internal adductor muscles was  $0.53 \pm 0.01$  and the IMA was  $0.62 \pm 0.02$ .

When slowly loaded, the external adductor system broke at  $3.09 \pm 0.16$  N; when rapidly loaded, the system broke at  $7.16 \pm 0.79$  N. Short duration loading at 2.0 N or more was found to result in histologically detectable damage at the pivot. When slowly loaded, the internal adductor system broke at  $0.68 \pm 0.05$  N. When a load of 0.39 N was applied to the internal adductor system, the failure point on slow loading of the external adductor system was not significantly increased.

The mean maximum force of contraction of the external adductor muscles on electrical stimulation was  $0.98 \pm 0.03$  N, with a stress of  $627 \text{ kN m}^{-2}$  in the fibres. The internal adductors contracted with a mean maximum force of  $0.33 \pm 0.01$  N. The total maximum bite force is therefore about 3.3 N, only 10% being contributed by the internal adductors. The safety factor of both internal and external systems is about 2.

The mean sarcomere length of half-contracted fibres of the external adductor muscles was  $11.62 \pm 0.11 \mu\text{m}$ .

### INTRODUCTION

The brachyuran mandible is a conservatively structured mouthpart, being closely similar in all true crabs. Its structure in *Cancer pagurus* L. was described by Pearson

\* Present address: Department of Biological Sciences, University of Science and Technology, P.M.B. 5080, Port Harcourt, Nigeria.

Key words: biomechanics, Brachyura, *Carcinus*, Crustacea, feeding, leverage, muscle, mandibles, safety factors, sarcomeres.

(1908) and in *Carcinus maenas* by Borradaile (1922). Manton (1964) described the operation of the mandibular system and, by demonstrating muscle homologies, showed that it could be derived from the astacuran system. The principle difference between the two lies in the relative importance of two sets of adductor muscles. The internal adductors, which originate medially on the roof of the carapace, are dominant in astacurans, whereas the external adductors, which originate laterally on the branchiostegites, dominate in brachyurans. The dominance of the external adductors in crabs is due partly to the relatively large size of these muscles, but also to their placement, on each side at the end of a long lever arm – the mandibular apophysis – room for which is provided by the crab's broad cephalothorax.

The brachyuran mandible thus constitutes an elegant lever system [of 'ultimate perfection' (Manton, 1977)] operated by two different sets of muscles which pull in different directions with different mechanical advantages (MA). Warner (1977) gave approximate measurements of MA for the internal and external adductors of *Cancer pagurus* – 0.4 and 1.3, respectively – and pointed out that contraction of the large external adductor, pulling at the end of the long apophysis, would stress the pivot. The articulation between each mandible and the epistome, which forms the pivot on each side, is an oblique hinge line of flexible tissue which allows rotation in one plane only. The pull of the external adductors is away from the pivot, tending to disarticulate the mandible from the epistome (see Fig. 1). Warner (1977) suggested that the internal adductors, which pull towards the pivot, might help to reduce the stress at the pivot caused by contraction of the external adductors, and so provide a safety mechanism helping to prevent disarticulation.

In this study of the operation of the crab mandibular system, attention was directed towards the concept of safety factors (Alexander, 1981). The problem was to compare the force required to break the system with that which could be generated by the muscles. Two other aspects of the system were also investigated: MAs of the lever systems and sarcomere lengths in the external adductor muscles. Functional MA, calculated from applied input and output forces, was compared with ideal MA (Brown, Cassuto & Loos, 1979) calculated from lever lengths. Sarcomere length measurements were taken to provide a check on the forces recorded from contracting muscles, since a rough relationship exists between force of contraction and sarcomere length (see Chapple, 1982, for review).

#### MATERIALS AND METHODS

##### *Mechanical advantage*

Freshly killed intermoult male crabs (carapace width 64–74 mm) were dissected by cutting the exoskeleton from above the base of one cheliped, up through the branchiostegite, across the cardiac region of the carapace, and down to the other cheliped. The part of the carapace with the epistome and mandibular units attached was then lifted away from the intact viscera. The preparation was held in a clamp and was kept moist throughout by a drip of *Carcinus* saline (Pantin, 1961) at room temperature. Small holes were made through the carapace at the point of origin of

each internal adductor muscle and through the branchiostegite on each side in line with the tip of each external adductor apodeme. Double-ply cotton thread was tied on to the point of attachment to the apophysis of the external adductor apodeme in one or both of the mandibles. The other end of the thread was passed through the hole in the branchiostegite in such a way that a pull on the thread simulated contraction of the external adductor muscle. The mandibular palp was cut off and a similar thread was attached to the centre of the cutting edge of the mandible by means of a drop of Permapond superglue. Using the same glue, thread was attached to each internal adductor apodeme to pull through the holes on the carapace and simulate contraction of the internal adductors.

Each thread passed over a Griffin XBD-690-V 4 cm diameter light alloy pulley orientated along the line of action of the simulated force. The 'output' force at the cutting edge of the mandible ( $F_2$ ) was pre-applied by a calibrated spring balance, causing the mandible to open fully. The 'input' force along one or other of the adductor muscle apodemes ( $F_1$ ) was applied by running water from a burette into a weighed plastic dish. All forces were applied using loads in g, and are converted to the appropriate units in the results assuming that a mass of 1 kg exerts a downward force of 9.8 N. The spring balance reading which corresponded to the mandible half closing (the balance point) was taken as the functional  $F_2$  in equilibrium with the applied  $F_1$ . The ratio  $F_2/F_1$  is the functional MA. Each external adductor preparation was loaded about 10 times with preset output loads increasing in regular steps from 15 to 105 g; internal preparations were loaded about five times with output loads from 10 to 25 g. Control experiments showed that the dissipation of force at the pulleys, spring balance and threads was negligible.

The ideal MA was estimated by measuring lever lengths on a sample of mandibles using a *camera lucida*. Each mandible was viewed, and lengths measured, as in Fig. 1A; viewing along the pivot was impractical as some parts were obscured and others out of focus. The ratio of the length of the input lever,  $L_1$ , to that of the output lever,  $L_2$ , is the ideal MA.

#### *Determination of failure loads*

Preparations were as described above, but both mandibles were used simultaneously and a metal dowel 2.5 mm in diameter was placed between the cutting edges of the mandibles to maintain a half-open gape. The external adductor apodemes were subjected to slow loading and to faster loading, while the internal adductors were subjected to slow loading only. During slow loading, water ran into the suspended containers at 3–5 ml min<sup>-1</sup> to give a steadily increasing  $F_1$  of equal magnitude on each side. Loading continued to failure, which occurred after 1½–2 h. Faster loading was achieved by replacing the containers with 1-kg spring balances. These were loaded evenly using screw clamps and loading time to failure was 5–10 min. A series of slow loading experiments was also carried out on the external adductors, with loads pre-applied along the internal adductor apodeme.

To investigate the possibility of damage to the pivot tissue at loads less than that causing breakage, the external adductor apodemes of seven preparations were loaded

on each side with 0 (control), 100, 200, 300, 400, 500 and 600 g for 5 min. The pairs of mandibles, still attached to their epistomes, were then fixed in formal saline for 24 h and decalcified in Gooding & Stewart's fluid (Mahoney, 1973) for 3–5 days with the solution changed twice daily. They were then dehydrated, cleared in chloroform and impregnated with molten wax; dehydration and embedding lasted about 48 h. 10  $\mu\text{m}$  serial transverse sections were taken across the hinge line of each mandible; these were stained in Masson's trichrome and examined for signs of fracture.

#### *Adductor muscle performance*

Large male crabs, as above, were rapidly dissected and semi-intact preparations were appropriately clamped to record the pull of the muscles. Preparations were constantly bathed in cool (10–15°C) aerated *Carcinus* saline from a saline drip. For the external adductors, the apophysis was cut and a thread was secured adjacent to the external adductor apodeme. For the internal adductors, the mandible was detached from the epistome and the apophysis cut; thread was secured to the gnathal lobe.

In each case the thread was extended under slight tension along the natural line of action of the muscle, and was attached to an aluminium bar on which a pair of 10/350 LY 13 fine strain gauges had been mounted using Araldite (Neubert, 1967). These were connected *via* a Wheatstone-bridge circuit to a Washington 400 MD 2R oscillograph. The dimensions of the bar (120×12×3 mm) were such that it sustained a very small deflection as the muscles contracted. The apparatus was calibrated after each experimental recording. Ag/AgCl electrodes insulated with lacquer except at the tip were used to stimulate the muscle fibres directly. A double pulse stimulator (SRI) was used at a frequency of 90 pulses  $\text{s}^{-1}$  at 25 V. Angles of pennation of the external adductor muscles with the mandibles half open were measured in other fresh specimens of the same size range, and areas of apodemes were measured using an overhead projector.

#### *Sarcomere length measurements*

Three large male crabs, as above, were dissected to expose the external adductor muscles, which were left intact. A 2.5 mm diameter metal dowel was put between the cutting edges of the mandibles to stretch the muscles to their half-contracted length, and the whole preparation was fixed in Bouin's.

Twenty fibres were sampled from each crab, five from the anterior and posterior blocks of each side. The fibres were finely teased and sarcomere lengths measured using a calibrated eye-piece graticule and phase-contrast microscopy. Preliminary observations gave no indication of differential contraction of sarcomeres within any fibre.

### RESULTS

Fig. 1 shows plan and side views of a mandible and a model of its operation. The simplicity of the model is evident, but the real lever system is complicated by the

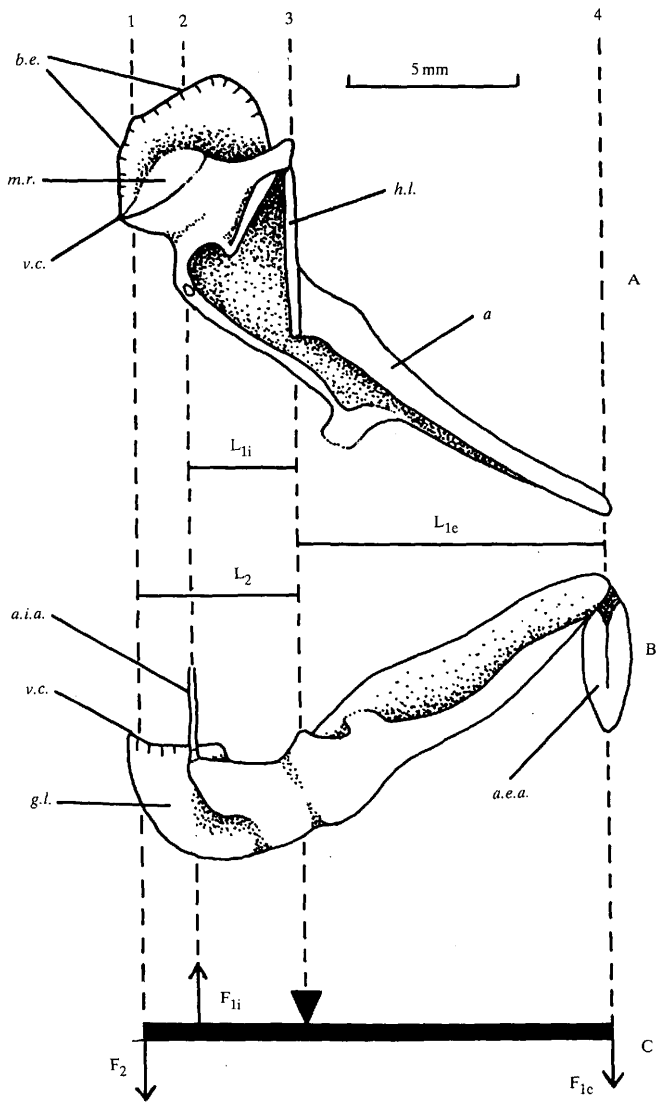


Fig. 1. Right mandible of *Carcinus maenas*. (A) Medial view at right angles to the hinge line; (B) ventral view parallel to the hinge line; (C) model of lever system. Dashed lines: 1, central point along the biting edge at which  $F_2$  was measured; 2, insertion of the internal adductor muscle apodeme; 3, pivot; 4, insertion of the external adductor muscle apodeme. Arrows indicate directions of forces acting on the mandible.  $L$ , lever lengths;  $F$ , forces; 1, input; 2, output; i, internal adductor; e, external adductor;  $a$ , apophysis;  $a.e.a.$ , apodeme of the external adductor muscle;  $a.i.a.$ , apodeme of the internal adductor muscle;  $b.e.$ , biting edge;  $g.l.$ , gnathal lobe;  $h.l.$ , hinge line;  $m.r.$ , molar region;  $v.c.$ , ventral cusp.

Table 1. Mean functional and ideal mechanical advantages (FMA and IMA) of the internal (i) and external (e) adductor muscles of the mandible, measured at the centre of the biting edge

	Mean	Range	N
FMA <sub>i</sub>	0.53 ± 0.01	0.47–0.57	5 (20)
IMA <sub>i</sub>	0.62 ± 0.02	0.55–0.67	8
FMA <sub>e</sub>	1.53 ± 0.01	1.29–1.68	9 (90)
IMA <sub>e</sub>	1.78 ± 0.03	1.68–1.92	8

N = mandibles (observations); standard errors and ranges are based on individual observations.

oblique line of the pivot, the three dimensional arrangement of the levers, and the fact that the pivot lines of left and right mandibles are not parallel but converge anteriorly. The shape of the gnathal lobe, however, is such that the right and left biting edges meet along their lengths when closed; the right mandible overlaps the left and enables food to be cut by shearing. Manipulation of food between the mandibles can be effected by the mandibular palps, situated dorsally, and some crushing may occur in the ventral molar region although these two regions do not meet at closure.

#### Mechanical advantage

No differences in mechanical advantage were found between left and right mandibles and although observed functional MA varied, the variation did not relate in any consistent way to the range of applied loads. Results were therefore combined (Table 1). It can be seen that the FMA of both internal and external adductor muscles is about 15% lower than the IMA. Since the measurements of FMA were static, the discrepancy is likely to be due to systematic errors in estimating lever lengths. Difficulties included exact location of the line of the pivot and correct orientation of the preparation.

#### Breakage

A summary of the mandibular loading experiments is given in Table 2 and shows three interesting features. First, the system can withstand a much higher load if this is applied rapidly. Second, when a load is applied along the internal adductor apodeme, the failure point due to overloading the external system is increased by

Table 2. Mean forces (Newtons) required to break the mandibular system ( $\pm$ S.E.)

Loading method	Mean input load at breakage	N	Location of break
Slow ext	3.09 ± 0.16	12	6p, 2e, 4ae
Faster ext	7.16 ± 0.79	6	3p, 1e, 2ae
Slow int	0.68 ± 0.05	5	5ai
Slow ext + load int	3.48 ± 0.09	4	3p, 1e

ext = external adductor system, int = internal adductor system, p = pivot, e = epistome, ae = apophysis, ai = internal adductor apodeme, + load int = a pre-applied load of 0.39 N on int.

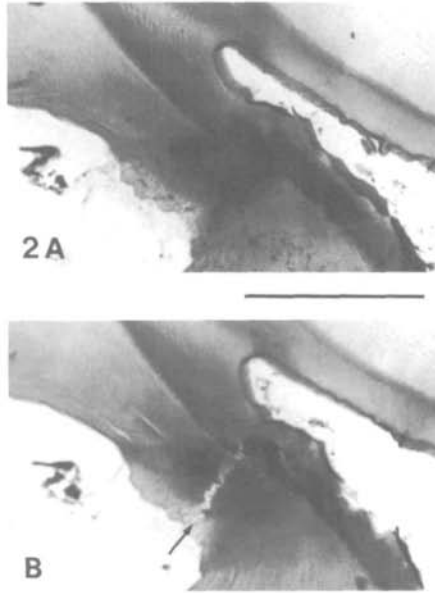


Fig. 2. Transverse sections across the hinge line of a *Carcinus* mandible loaded with 200 g at the insertion of the external adductor muscle prior to processing. The epistome is above, the pivot tissue on the hinge line is central and the mandible is below. (A) No damage detectable in this section; (B) small tear (arrow) visible in the pivot tissue.

about 12%. This increase was not statistically significant, but is in the expected direction. Third, it was expected that loading the external system would cause a break at the pivot, since this was assumed to be the weakest point. Although this was often the case, breaks also occurred elsewhere, revealing a certain design consistency – the strengths of the various parts matched each other.

The results obtained from histological examination of the hinge line in mandibles to which sub-failure loads were briefly applied were that all preparations loaded with 300 g or more showed conspicuous tearing of pivot tissue along the hinge line. A single small tear was also found in the preparation loaded with 200 g (Fig. 2). No damage was found at any load lower than 200 g.

#### *Force and stress in the muscles*

Table 3 shows a summary of the maximum forces recorded on electrical stimulation of the adductor muscles. Stress in the muscle (S) can be calculated from the formula of Alexander (1969)

$$S = F/A \sin 2\theta,$$

where  $F$  is the force produced by the muscle at the insertion of its apodeme,  $A$  is the area of the apodeme and  $\theta$  is the angle of pennation of the fibres onto the apodeme. This calculation was performed for external adductors only, since the shapes of the internal adductor and its apodeme do not allow the necessary measurements to be taken.

Mean external apodeme area for crabs in this size range was found to be  $3.851 \pm 0.013 \text{ mm}^2$  ( $N = 10$ ). Pennation angles, however, were found to vary widely both between and within the anterior and posterior blocks of muscle inserting on the anterior and posterior faces of the apodeme. Fibres on the anterior face were normally  $< 10 \text{ mm}$  long and pennated at  $10\text{--}25^\circ$ , whereas those on the posterior face were  $> 10 \text{ mm}$  long and pennated at  $2\text{--}15^\circ$ . By measuring the angles of equal numbers of fibres on both sides of three different preparations, a mean of  $12.3 \pm 1.0^\circ$  ( $N = 30$  fibres) was calculated. Using these data, and the mean force in Table 3, the mean maximum stress in the external adductor fibres was found to be  $627 \text{ kN m}^{-2}$ .

#### *Sarcomere length*

Only the external adductor muscles were studied. No differences were found between left and right sides, or between anterior and posterior blocks of muscle. Results were therefore combined and yielded a mean sarcomere length for half contracted fibres of  $11.62 \pm 0.11 \mu\text{m}$  ( $N = 60$  fibres). The range for individual fibres was  $10.54\text{--}14.24 \mu\text{m}$ .

#### DISCUSSION

The mandibular adductor levers have high MAs adapted to the biting action of the mandibles. Biting requires neither extensive movement nor great speed, but it does need to be forceful, and this is achieved by the long apophysis which steps up by one and a half times the force produced on either side by the external adductor muscles. MAs reported from various reptant crustacean chelae are much lower, ranging from 0.16 for the cutter chela of the lobster *Homarus americanus* Milne-Edwards (Elner & Campbell, 1981) to 0.55 for the crab *Daldorfia horrida* (L.) (Vermeij, 1977). Chelae are more versatile appendages than mandibles, and chela MA can be greatly increased by moving the object to be pinched closer to the pivot (Warner, 1977). The capacity for further increasing the mandibular MA is, by comparison, limited.

The difference in the failure loads on slow and faster loading demonstrates the existence of a viscous component which may increase toughness under normal usage.

Table 3. Mean maximum forces (Newtons  $\pm$  S.E.) along their apodemes produced by contraction of the mandibular adductor muscles, induced to contract by electrical stimulation

	Mean force	Range	<i>N</i>
External	$0.98 \pm 0.03$	0.83–1.08	7
Internal	$0.33 \pm 0.01$	0.27–0.37	7



Evidence from the histological study, however, showed that some fracture of the pivot tissue occurs at loads lower than those causing breakage. It is, of course, quite unnatural for the adductor muscles to contract with a steadily increasing force for up to 2 h, as in the slow loading experiments. Short pulses of contraction were found by Wales, Macmillan & Laverack (1976) for mandibular adductor muscle activity in *Homarus gammarus* (L.), where a normal cycle of close-bite-open lasts 2–3 s with some variability depending on food type (Macmillan, Wales & Laverack, 1976). Thus even the faster and short duration loading experiments involved much longer load applications than crabs are likely to inflict upon themselves during feeding.

The maximum forces produced by contracting adductor muscles show that the crude safety factor of both internal and external systems is about 2. In view of the unnaturalness of the loading experiments, the operational safety factor may be rather higher. A factor of 2 is, however, similar to safety factors found for other arthropod cuticular structures, the range being from 1.2 for the locust extensor apodeme to 4 for the plastron of a water bug (cited by Alexander, 1981). Crab mandibles are partly internal and partly sheltered by surrounding mouthparts, they are therefore unlikely to experience accidental stress, and it could be argued that 2 is an unnecessarily high safety factor (see Alexander, 1981). However, moulting involves periodic weakening of the cuticle and it is possible that early recommencement of feeding after moulting may be possible with 'overdesigned' mandibles.

Calculation of the expected stress at the pivot using the MA data in Table 1 and the maximum force of contraction data from Table 3, shows that contraction of the internal adductor muscles should reduce stress at the pivot by about 9% at maximum bite. In view of the high overall safety factor, however, it must be concluded that this is insignificant in preventing breakage. The contribution of the internal adductors to the bite force is also rather small. From Table 1 and Table 3, a maximum bite of about 3.3 N can be calculated, only 10% of which is due to the internal adductors.

The mean maximum stress of  $627 \text{ kN m}^{-2}$  calculated for contracting external adductor muscles is similar to those previously reported for whole crustacean muscles made up largely of slow fibres. These range from  $390 \text{ kN m}^{-2}$  for lobster major chela closer muscle (Elner & Campbell, 1981) to  $748 \text{ kN m}^{-2}$  for *Carcinus* major chela closer muscle (Abby-Kalio & Warner, 1984). The forces produced by these whole muscles are assumed to be maximized at half contraction. This assumption derives from expectations based on length-tension curves for individual fibres. However, as pointed out by Chapple (1982), peak tension in fibres may occur at points other than half-contraction. In whole crustacean muscles, the position is further complicated by the fact that the fibres pennate at a range of angles and may also be of different lengths (Warner, Chapman, Hawkey & Waring, 1982; present investigation). For a given movement of their insertion, short fibres and fibres pennating at small angles contract through a greater proportion of their length than do long fibres or those with larger angles of pennation. Thus, for a given whole muscle contraction, individual fibres may be at different states of contraction and at different points along their individual length-tension curves. It is possible that the observed diversity of fibre length and angles of pennation allows whole muscles to

sustain high tension over a greater operational range than would be expected from a simple extension of length-tension curve data (see Chapple, 1982).

The sarcomere length measurements for the external adductors show more uniformity than is seen in chela closer muscles (Warner & Jones, 1976; Warner *et al.* 1982) or in the muscles of other head appendages such as the first antenna (Reger, 1967) and the eyestalk (Hoyle & McNeill, 1968). Most noticeably there are no fibres with short sarcomeres. Uniform slow muscle capable of contracting forcefully is as expected in these specialized appendages.

#### REFERENCES

- ABBY-KALIO, N. J. & WARNER, G. F. (1984). Effects of two different feeding regimes on the chela closer muscles of the shore crab, *Carcinus maenas* (L.). *Mar. Behav. Physiol.* **11**, 209-218.
- ALEXANDER, R. MCN. (1969). Mechanics of the feeding action of a cyprinid fish. *J. Zool., Lond.* **159**, 1-15.
- ALEXANDER, R. MCN. (1981). Factors of safety in the structure of animals. *Sci. Prog., Oxford* **67**, 109-130.
- BORRADAILE, L. A. (1922). On the mouth parts of *Carcinus maenas* (L.). Decapoda: Portunidae. *J. Linn. Soc. (Zool.)* **35**, 115-142.
- BROWN, S. C., CASSUTO, S. R. & LOOS, R. W. (1979). Bio-mechanics of chelipeds in some decapod crustaceans. *J. Zool., Lond.* **188**, 143-159.
- CHAPPLE, W. D. (1982). Muscle. In *The Biology of Crustacea*, vol. 3 (ed. H. L. Atwood & D. C. Sandeman), pp. 151-184. New York, London: Academic Press.
- ELNER, R. W. & CAMPBELL, A. (1981). Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapoda: Crustacea). *J. Zool., Lond.* **193**, 269-286.
- HOYLE, G. & MCNEILL, P. A. (1968). Correlated physiological and ultrastructural studies on specialised muscles: Ib ultrastructure of white and pink fibres of the levator of the eye stalk of *Podophthalmus vigil* (Weber). *J. exp. Zool.* **167**, 487-522.
- MACMILLAN, D. L., WALES, W. & LAVERACK, M. S. (1976). Mandibular movements and their control in *Homarus gammarus*. III. Effects of load changes. *J. comp. Physiol.* **106A**, 207-221.
- MAHONEY, R. (1973). *Laboratory Techniques in Zoology*. London: Butterworth & Co.
- MANTON, S. M. (1964). Mandibular mechanisms and the evolution of arthropods. *Phil. Trans. R. Soc. Ser. B* **217**, 1-183.
- MANTON, S. M. (1977). *The Arthropoda*. Oxford: Oxford University Press. 527pp.
- NEUBERT, H. K. P. (1967). *Strain Gauges: Kinds and Uses*. London: Macmillan. 164pp.
- PANTIN, C. F. A. (1961). *Notes on Microscopical Techniques of Zoologists*. Cambridge: Cambridge University Press. 77pp.
- PEARSON, J. (1908). *Cancer. Mem. Liverpool mar. Biol. Committee* **XVI**, 1-209.
- REGER, J. F. (1967). A comparative study of striated muscle fibres of the first antenna and the claw muscle of the crab *Pinnixia* sp. *J. ultrastruct. Res.* **20**, 72-82.
- VERMEIJ, G. J. (1977). Patterns in crab claw size: the geography of crushing. *Syst. Zool.* **26**, 138-151.
- WALES, W., MACMILLAN, D. L. & LAVERACK, M. S. (1976). Mandibular movements and their control in *Homarus gammarus*. II. The normal cycle. *J. comp. Physiol.* **106A**, 193-206.
- WARNER, G. F. (1977). *The Biology of Crabs*. London: Elek Science. 202pp.
- WARNER, G. F., CHAPMAN, D., HAWKEY, N. & WARING, D. G. (1982). Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). *J. Zool., Lond.* **196**, 431-438.
- WARNER, G. F. & JONES, A. R. (1976). Leverage and muscle type in crab chelae (Crustacea: Brachyura). *J. Zool., Lond.* **180**, 57-68.