

MOTOR PERFORMANCES OF SOME CEPHALOPODS

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It has long been recognized that contraction of the mantle muscles of a pelagic cephalopod produces high hydrostatic pressure in the mantle cavity, a jet of water from the funnel and movement of the animal in the opposite direction (Fig. 1). As a result of their investigation of the responses of squid muscle to repetitive stimulation of giant nerve fibres, Prosser & Young (1937) considered that the expulsion of each jet of water, occurring in locomotion, is a single unitary act which is performed in an all-or-nothing

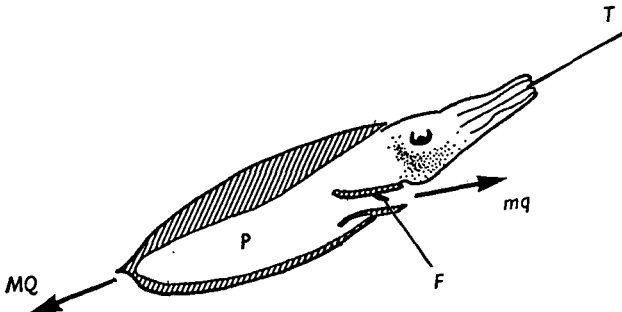


Fig. 1. Diagram of *Sepia* showing method of attachment to a myograph by a thread hooked into the base of the arms to record the tension (T) developed during swimming. The pressure (P), generated by the contraction of the mantle muscles and recorded by a cannula joined to a pressure transducer, produced a jet from the funnel (mq) which imparts momentum to the animal (MQ). F , valvular flap near the mouth of the funnel.

manner. Absence of any increased response in fresh muscle preparations at higher frequencies showed that a single nerve impulse carried by a giant axon is capable of activating every muscle fibre that it reaches. In parallel with the decapod fast system there is a slow system made up of many small-diameter nerve fibres, which when stimulated provoke smaller graded muscular contractions in a mantle preparation (Young, 1938). This author assumed that these graded contractions produced the mantle movements involved in respiration. The graded contractions were further studied by Wilson (1960) who demonstrated that *Octopus* (*O. bimaculatus* and *O. bimaculoides*) also have a fast and a slow system. The fast system of *Octopus*, unlike that of the decapods, shows marked facilitation of the mechanical response and a single twitch takes 160 m.sec. to reach maximum tension. Summation of *Octopus* fast and slow systems and of the squid slow response take place in a two-phase manner, a rapid increase in tension being followed by a slower rise.

The responses discussed above are all due to the contraction of the circular muscle fibres of the mantle causing water expulsion, the fast system being used in locomotion, the slow in respiration. It is generally agreed that the expansion of the mantle, bringing about the intake of water, is due to the radial muscle fibres but it has not been easy to

differentiate their response from the much stronger contractions of the circular muscles (Young, 1938; Wilson, 1960).

Apart from the above work and papers by Prosser & Young (1937) and Dilly, Nixon & Packard (1964), little has been written on the motor performances of cephalopods. In the present research it was hoped that observations of the pressure pulses produced in the mantle cavity would allow some assessment of the nature of the muscle response in the intact animal. We have paid particular attention to the relationship between pressures developed in the mantle cavity and their locomotory power, discussing some of the factors affecting this. *Sepia officinalis* (L.), *Loligo vulgaris* Lamarck, *Eledone moschata* (Lamarck) and *Octopus vulgaris* Lamarck were studied, using electronic recording techniques (Hoggarth & Trueman, 1967), and some comparison is made between them.

METHODS

Recordings of pressure were made on fresh animals using a multi-channel pen recorder (physiograph, E. and M Instrument Co. Inc.) with Statham and linear core pressure transducers. The principal difficulty experienced was in retaining a pressure cannula within the mantle cavity of an active cephalopod when swimming in a large tank. It was found convenient to narcotize the animal lightly in urethane and to stitch a nylon thread through the cranial cartilage so as to suspend it in a suitable position in the tank. Alternatively a metal hook was introduced, without narcotization, between the arms. To enable pressures to be recorded a cannula was inserted through a small hole cut in the mantle while narcotized, but similar pressures were obtained with the cannula gently inserted through the inhalent aperture of the mantle cavity and held there by hand. This method had the advantage of not damaging the mantle tissues but required rather long and flexible tubing between the cannula and the pressure transducer. Normally 60 cm. of rubber pressure tubing (3 mm. bore) was used but, as our technique improved, we were able to utilize thin polythene tubing (15 cm. long) with similar results. Allowance has been made in the interpretation of the recordings for the delay due to the tubing used. This was determined by applying pressure, of similar amplitude to the pulses recorded, to the cannulae and tubing employed.

The thread attached to the animal not only restricted the swimming movements but also allowed the tension (Fig. 1, T) developed by jetting to be recorded by means of an isometric myograph simultaneously with pressure. The difficulty in using this technique to record the thrust developed is that the animal must swim directly or obliquely downwards. In this respect *Sepia* was the best performer, since it tends to swim down, and *Eledone* and *Loligo*, which swim more horizontally, gave rather low values. The myograph was put out of action by splashes if placed too near the surface of the water and it proved difficult to align the thread with the direction of the jet.

Determinations of mantle capacity (Table 1) were made immediately following the death of the animal by filling the mantle cavity with water. These passive measurements are less than can be achieved by the actively stretched mantle in life, the water expelled from *Eledone* on removal from the aquarium being one-third greater than the passive volume. However, repeated observations of jet swimming suggest that the passive mantle capacity can be taken as the maximum amount of water normally expelled at each vigorous swimming stroke. The areas of cross-section of the jets as

cited (Table 1) are derived from measurements of diameter of the funnel in the living or freshly dead animal; but the funnel aperture alters during the development of the jet in a way which it has not so far been possible to assess.

Table 1. Comparison of factors concerned with jet propulsion in certain cephalopods

| Species | Wet weight (g.) | Cross-sectional area of jet (A , cm. ²) | Mantle capacity (V , ml.) | Pressure pulse duration (t , msec.) | Velocity of jet (q , cm./sec.) | Theoretical maximal velocity of animal during single jet cycle (Q , cm./sec.) | | | |
|--------------------------|-----------------|--|------------------------------|--|-----------------------------------|--|------------------------------|------------------------------|------------------------------|
| | | | | | | Mantle water all expelled | $\frac{2}{3}$ water expelled | $\frac{1}{2}$ water expelled | $\frac{1}{3}$ water expelled |
| <i>Octopus vulgaris</i> | 370 | 0.7 | 53 | 600 | 126 | 18 | — | — | — |
| <i>Eledone moschata</i> | 600 | 1.6 | 300 | 200 | 940 | 470 | 177 | 94 | 40 |
| <i>Loligo vulgaris</i> | 350 | 1.5 | 200 | 180 | 730 | 420 | 155 | 81 | 33 |
| <i>Sepia officinalis</i> | 250 | 1.5 | 62 | 150 | 275 | 68 | 27 | 15 | 0.6 |

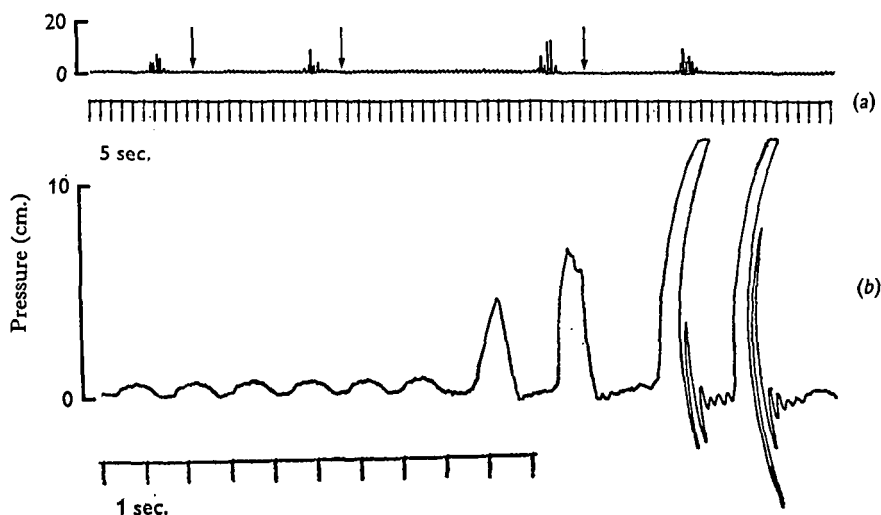


Fig. 2. Pressure recordings (in cm. of water) from within the mantle cavity of (a) *Octopus* (40 g. wet weight), and (b) *Sepia* (220 g.). In (a) the animal was at rest, showing a regular respiratory rhythm with short periods of hyperventilation, at the regular frequency, followed by depression in amplitude (arrows). In (b) the respiratory rhythm was broken by development of jets of increasing amplitude. Oscillations occurring after the last two high pressures are due to the effect of sudden reduction in pressure on the Statham transducer.

EXPERIMENTAL RESULTS

(a) Respiratory rhythm

Pressure recordings from the mantle cavity afforded a means of monitoring respiratory activity. Fig. 2a is a typical extract of such a recording from an octopus of 40 g. wet weight at rest at the bottom of a tank and shows a regular rhythm at a rate of 29/min. which continues unchanged through periods of hyperventilation. After the latter the amplitude of respiration is somewhat reduced (arrows). A similar recording of *Sepia* (220 g.) shows the respiratory rhythm of 44/min. at rest broken by jetting of increasing amplitude. Observations made simultaneously with pressure recordings indicated that

the valvular flap in the funnel of *Sepia* was closed as the pressure increased and opened as the pressure fell. When the pressure is raised the mantle appears more swollen and the inhalent channels are effectively blocked by the outer collar of the funnel which is distended by water pressure and locks into the cartilaginous sockets of the mantle. This mechanism ensures that water passes out through the funnel and is particularly effective at the higher pressures encountered during swimming. Any tendency for the water to escape at the inlet is further offset by the head and funnel retractors which pull on the dorsal part of the mantle bringing the edges of the inlet up against the back of the head.

Previous recordings of the respiratory pressures appear to be limited to the report of Johansen & Martin (1962) who observed the effect of respiratory movements on the circulation of the blood of *Octopus dofleini*. These authors demonstrated the importance of the respiratory pump as an auxiliary means of blood propulsion by pressure tracings recorded from the great veins. The respiratory pressure pulses showed a frequency of about 8/min., range from 1 to 17 cm. of water pressure with a pulse pressure of 3–5 cm. In the animals used in the present work the pulse pressure is less than 1 cm. and of much higher frequency. This is in keeping with their small size in comparison with the 1–30 kg. *O. dofleini* used by Johansen & Martin. It would seem unlikely that the normal respiratory rhythm in *Sepia* and small *Octopus* is an important factor in the circulation of the blood but the possibility of hyperventilation being effective in this respect should be further investigated.

(b) High-pressure pulses

In all the cephalopods here investigated high pressure-pulses could be recorded from the mantle cavity (Fig. 3), a maximum of 400 cm. of water being obtained from an *Eledone* of 600 g. wet weight. Maximal peaks are notable for their sharp rise and fall, having a duration of about 150 msec. in *Sepia*. Following the pulse the sudden fall in pressure commonly set up oscillations in the unloaded pressure recording system (Fig. 3a, c) and prevented critical observations after the formation of the jet when a slight negative pressure might be expected to correspond to the expansion of the mantle cavity.

Simultaneous observations of pressure in the mantle cavity and in the mouth of the funnel with the cannula held just outside the valvular flaps (Fig. 1) showed high-pressure pulses of equal amplitude. The duration is slightly greater in the mantle, and the funnel pulse is delayed about 60 msec. after the development of pressure in the mantle cavity (Fig. 4). It would appear likely that the pressure builds up in the mantle cavity and is released by the opening of the funnel possibly in the same manner as in respiratory exhalation.

(c) Recordings of pressure and tension

Simultaneous recordings of pressure and tension afford a means for comparing the jet pressures and their locomotory thrust. The coincidence of changes in both pressure and tension was observed in many recordings such as those in Fig. 3 and comparison was only limited by the maximum speed of the pen recorder. The traces show that the maximum tension developed in *Sepia*, *Loligo* and *Eledone* is approximately equivalent to their body weight; *Octopus*, on the other hand, only produces a tension of about one-half of the body weight. The tension recorded is due not only to the jet but also to

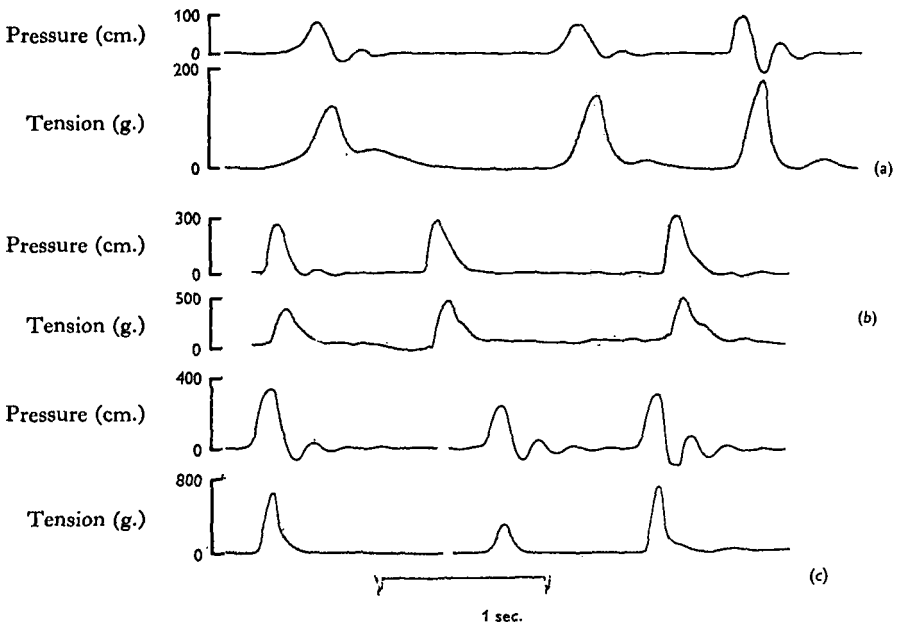


Fig. 3. Simultaneous recordings of pressure and tension in (a) *Sepia* (260 g.), (b) *Loligo* (400 g.) and (c) *Eledone* (600 g.) obtained in the manner indicated in Fig. 1. The pressures for *Sepia* were recorded from the mouth of the funnel, the others from within the mantle cavity.

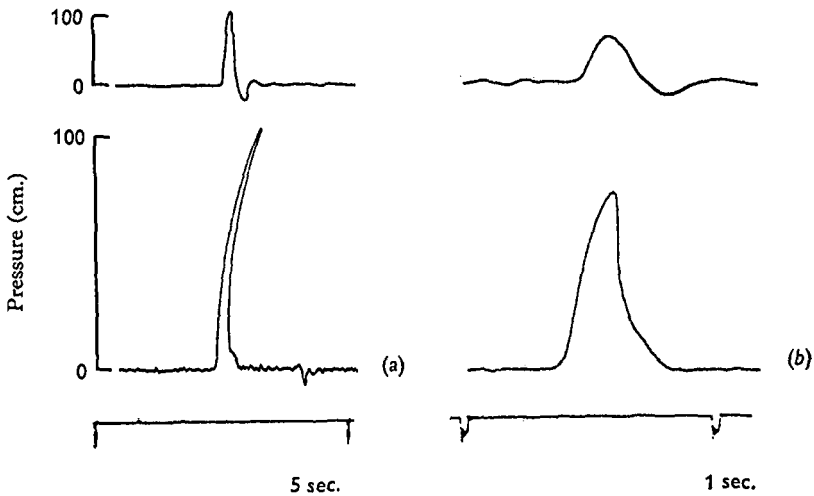


Fig. 4. Simultaneous recordings of high pressure within the mouth of the funnel (above, using linear core pressure transducer) and mantle cavity (below, using Statham transducer). The pressure in the former is delayed by about 60 msec. after its development in the mantle cavity.

swimming with the fins in *Sepia* and *Loligo* and with the arms in *Octopus*. This probably accounts for the irregularities in the base line for tension for *Sepia* (Fig. 3a). In *Loligo* the relatively powerful fin muscles, which weigh one-quarter as much as the mantle muscle, are innervated by nerves of central origin which do not synapse in the stellate ganglion; film analysis of squid swimming suggests that the fins make their downstroke immediately before jet output. This shows up in the recordings of tension (Fig. 3b) as a small hump immediately preceding the peak. The fins are thus momentarily unavailable for steering and this may account for the relatively low values of tension recorded for *Loligo*.

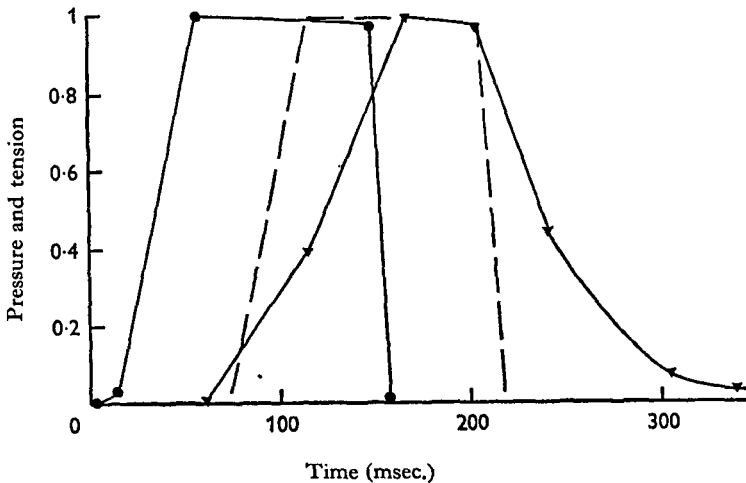


Fig. 5. Graph showing relation between the pressure in the mantle cavity (●—●) and tension (▼—▼) for a single jet produced by *Sepia* (250 g.) corrected for the arc of the recording pens and the delays in the recording system. Pressure and tension are expressed as fractions of the maximum developed (180 cm. and 350 g. respectively). The broken line represents the same pressure peak delayed by 60 msec.

The relation between pressure and tension is further obscured because of the arc drawn by the recorder pens and can be seen more clearly through an analysis of a single pressure and tension pulse for *Sepia* (Fig. 5). The steepness of rise and fall of the pressure may only be fully appreciated on such a graph. The tension reaches its maximum as the pressure in the mantle cavity is falling steeply, but if the pressure occurring at the mouth of the funnel is considered there is a much closer relationship particularly as the pressure pulse begins to fall. The funnel pressure was not recorded simultaneously with the tension and mantle cavity pressure used to construct Fig. 5 but is indicated (broken line) in the position to be expected from other recordings such as Fig. 4b. The duration of the curve for tension is rather longer than that for pressure, commencing before and terminating after the pressure pulse in the funnel. This is probably due to the fins supplementing the water jet.

(d) Analysis of results

The quantitative relationship between pressure (P) and tension (T) can be shown more clearly in graphs, plotted for different animals, from the data of numerous recordings such as shown in Fig. 3. These confirmed that the maximum tension

produced was equivalent to the body weight except in *Octopus* where it was one-half of this. Regression lines have been drawn in respect of the points plotted, and from these it may be deduced that T is proportional to $3.1P$ for *Sepia*, $2.6P$ for *Eledone*, $1.45P$ for *Loligo* and $0.54P$ for *Octopus*. The momentum (I) derived from a jet is equal to twice the force which would have been exerted by a difference in pressure (P) on a piston with the same cross-sectional area (A) as the jet (Prandtl, 1952). This is $I = 2AP$. If the momentum produced is equivalent to the tension recorded on the myograph then the condition $T = 2AP$ should hold. This relationship is shown in Fig. 6 by a

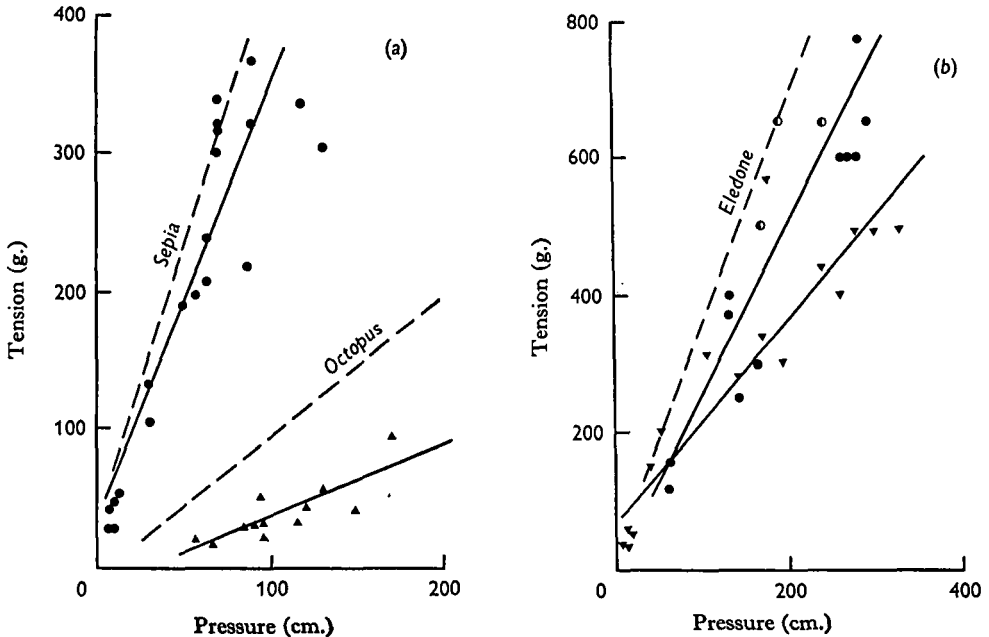


Fig. 6. Graphs showing the relationship between pressure and tension in (a) *Sepia* (340 g.) (●) and *Octopus* (220 g.) (▲) (b) *Eledone* (600 g.) (●) and *Loligo* (400 g.) (▼), data from recordings similar to those shown in Fig. 3. Regression lines determined by method of least squares; ●, jets occurring in response to d.c. stimulation of the arms of *Eledone*. The broken lines indicate the relationship $T = 2AP$ for the animal named.

broken line for each species, that for *Loligo* being almost the same as *Eledone*. The regression lines do not correspond to these, possibly because of points to the right of the line, which represent occasions when the tension was not fully developed on the myograph, some of them because the direction of swimming was not completely aligned with the myograph thread. The values of pressure, on the other hand, are correct readings so that the relationship between pressure and tension is most probably indicated by lines passing through the points on the left of each graph. These would closely approximate to the broken lines in Fig. 6 for all species examined except *Octopus* where the tensions recorded are considerably lower than might be expected. The swimming ability of *Octopus* is discussed in the next section.

This comparison has been made on the basis of the amplitude of pressure and tension peaks, i.e. pulse heights, and a more valid comparison may be obtained by determining the areas beneath the peaks. The area under the pressure-time curves is

a measure of the tension developed by the contraction of the mantle muscles while that beneath the tension-time curves is equivalent to the total impulse of the fluid ejected from the mantle cavity. The area beneath pairs of pressure and tension peaks was determined for *Sepia*, *Loligo* and *Eledone* and produced similar graphs to those shown in Fig. 6, bearing the same relationship to the formula, $T = 2AP$.

Measurement of weight, cross-sectional area of jet (A) mantle capacity (V) and the duration of the pressure pulse (t) allow the velocity of the jet to be determined on the assumption that the passive mantle capacity represents the total volume of water expelled at each pressure pulse.

Velocity of the jet

$$(q) = \frac{V}{At}.$$

Table 1 indicates that maximal jet velocities are attained in *Loligo* and *Eledone* in association with relatively greater mantle capacities than in *Sepia* or *Octopus*. Such jet velocities are probably developed in association with the maximum pressures of 300 and 400 cm. of water recorded respectively in *Loligo* and *Eledone*. Some estimate of the maximal velocity of the animal may be made on the basis of the velocity and volume of the jet (m) since:

Momentum imparted (I) = $mq = MQ$, where M is the mass of the animal and Q , its velocity. The mass of the animal has been determined as its wet weight but the effective mass of the animal should also include the skin of water carried along with it, estimated by Lang (1966) for dolphins to be as much as 10% of body weight, and the residual water in the mantle cavity. These factors and the effect of drag have not been allowed for here except in respect of the calculation concerning the partial emptying of the mantle cavity. Ejection of all the mantle water, making m maximal, leads to high velocities in *Eledone* and *Loligo* but only a very low velocity in *Octopus*. Reduction in jet output not only reduces the momentum imparted but also raises the effective mass of the animal and proportionately reduces its velocity. Values with the ejection of different proportions of the mantle capacity are given for comparative purposes in Table 1 and indicate that *Loligo* and *Eledone* may attain a high speed with use of only half of their mantle capacities. Estimation of the speed of *Sepia* (250 g.) from cine film during $\frac{1}{8}$ th sec. after jetting gave a speed of 80 cm./sec. whilst Packard's (1966) determinations, using stroboscopic photography, for a 3 g. *Loligo* gave a maximum of 120 cm./sec. and more recently (1968) for a 100 g.-animal, 210 cm./sec. from a standing start. Having regard to the size of these squids, the values given in Table 1 for velocity are comparable provided that the volume of water ejected from the mantle cavity approaches its total capacity as determined passively in *Sepia*, or two-thirds of this in *Loligo*.

From the values of maximal velocity given in Table 1 it is possible to determine the average acceleration of these cephalopods on the assumption that the time from rest to maximum speed is the same as the width of the pressure pulse, for after the jet is completed they must decelerate. Using the data from Table 1 the acceleration of *Sepia* is 400 cm./sec.², *Eledone* 2350, *Octopus* 30 and *Loligo* 2330 or with a 3 g. animal 1700 (data from Packard, 1966). This further emphasises the poor swimming ability of *Octopus*.

(e) Motor performances of *Octopus*

In the previous section reference has been made to the fact that the octopus is a poor swimmer, for it cannot maintain its direction when jetting nor is its body highly streamlined. Fig. 7 shows the swimming pulls of a series of small *O vulgaris* as a function of body weight. The maximum tension exerted when swimming was never more than half body weight and compares unfavourably with tensions similar to body weight recorded from the other cephalopods. This poor performance must be related to the small size of the mantle and mantle capacity. The total mantle musculature of

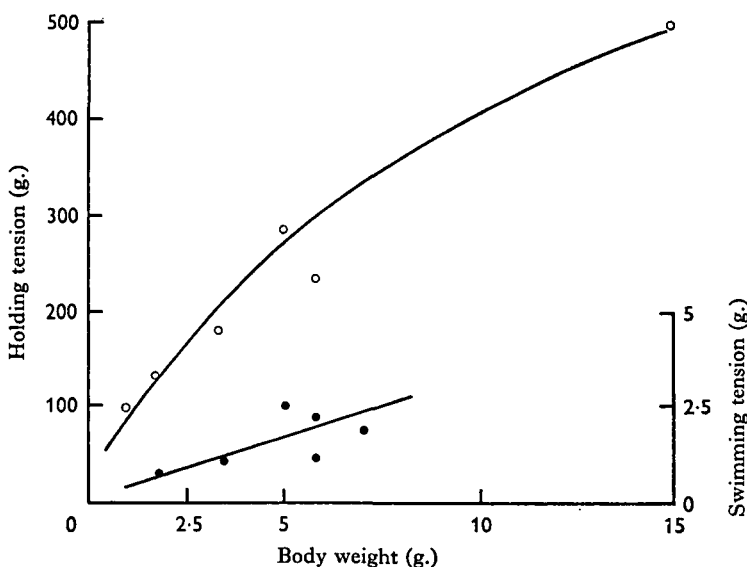


Fig. 7. Graphs showing relationship between the increase in the body weight of young *Octopus*, the maximum tensions developed by production of jets (swimming tension, ●) and the maximum holding pull (holding tension, O) with five arms attached to the bottom of the tank. The latter represent points at which a thread stitched through the cephalic cartilage broke free.

a 370 g. octopus is 8% of body weight compared with 47% for mantle and fins in a 235 g. *Loligo*. On the other hand the arms of *Octopus* occupy from 56% of body weight in animals of less than 1 g. to 70% in those of over 1 kg. (Dilly, Nixon & Packard, 1964). The maximum tensions developed by the small octopuses when holding onto the side of the experimental tank with five arms is also shown in Fig. 7. These records were made at the same time as the swimming pulls with the animals pulling on a thread fixed into the cranial cartilage. On occasions when the octopus succeeded in breaking the thread these pulls were considered as being maximal. The holding tensions show just how powerful are the arms in comparison to the mantle musculature. An octopus of 1 g. body weight pulled just over 100 g. which, taking into account the the cross sectional area of the longitudinal muscles at the base of the eight arms, represents a muscular tension of 2 kg./cm.².

The muscular development and the essentially bottom-living habits of the octopus

are reflected in the statement that while the swimming pulls of the small animals used are less than half the body weight the holding pulls using five arms are between 30 and 100 times the body weight.

DISCUSSION

In a brief discussion of swimming in cephalopods Morton (1964) comments that the chief evolutionary preoccupation in the evolution of modern coleoids has been the attainment of speed, streamlining and fins. Although streamlining is closely related to the attainment of high velocities, the most important factors are the velocity and mass of water ejected from the mantle cavity and the rate at which this mass attains maximum velocity. These are affected by the following: (a) the musculature of the

Table 2. *Comparison of mantle capacity and musculature in adult cephalopods*

| | Mantle capacity as % of body weight | Mantle muscle weight as % of body weight | Average mantle thickness (cm.) |
|--------------------------------------|-------------------------------------|--|--------------------------------|
| Octopoda | | | |
| <i>Octopus vulgaris</i> (370 g.) | 10 | < 10 | 0.22 |
| <i>Eledone moschata</i> (600 g.) | > 50 | 20 | 0.64 |
| Decapoda | | | |
| <i>Loligo vulgaris</i> (350 g.) | > 50 | 35 | 0.52 |
| <i>Sepia officinalis</i> (250 g.) | 20-30 | 30 | 0.75 |

mantle and its contractile properties, for these determine the pressure that may be generated; (b) the cross-sectional area of the funnel, the velocity of the jet being inversely proportional to its area; (c) the volume of the mantle cavity. (a) and (b) may both affect the velocity of the jet while (c) may restrict the mass of water ejected. Table 2 compares the adult mantle muscle weight and capacity in the four species used in these experiments. The weight of muscle was determined after dissection from the animal and the removal of all skin and subcutaneous tissues; its average thickness was arrived at by laying out the cut mantle on squared paper and dividing this value into the volume of the muscle as found by displacement. If the mantle capacity is small the pressure pulse must be of short duration or of small amplitude. There is clearly adaptive value in having a large mantle cavity and powerful (thick) mantle muscles as occur in *Eledone* and *Loligo*. Jet propulsion favours animals with large body size and it has been suggested that this accounts for the rapid growth rate of cephalopods (Packard, 1966).

Table 2 emphasizes the poor development of the mantle muscles of *Octopus*. In this genus a smaller mantle capacity is associated with a pressure pulse of longer duration than observed in the other cephalopods (Table 1) and these account for the low velocity determined for the jet of the octopus. This jet velocity leads to a theoretical maximum body velocity during a single jet cycle considerably below the speed that those familiar with the animal would estimate. It should, however, be remembered that we are here dealing with speed from a standing start whereas many observations of higher speed

will normally have involved a succession of jet cycles. Improved performance can be attained by reduction of the cross-sectional area of the jet. This would increase jet velocity and affect the relationship between tension, pressure and jet area ($T = 2AP$) indicated by the broken line in Fig. 6*a*. A reduction of the jet area by one-half would make the latter almost correspond to the regression line drawn for *Octopus* and would double the jet velocity cited in Table 1. In most hydrodynamic examples of jets the cross-sectional area of the jet is less than that of the orifice through which the fluid flows, this phenomenon being known as contraction (Prandtl, 1952). The values of funnel cross-sectional area used in the velocity determinations (Table 1) do not allow for this factor and further observations on the formation and nature of the jet would be of great interest. It would be equally interesting to find out how the radial muscle fibres cause mantle expansion and water to be drawn into the mantle cavity.

It is possible to make an approximate determination of the muscle tensions involved in the production of a pressure pulse by use of the method of Batham & Pantin (1950) to determine the tension in the muscles of a sea anemone. For a cylinder of infinite length the tension per cm. in its wall, across a line parallel to its axis, is equal to the internal pressure multiplied by the radius of the cylinder. The mantle cavity is obviously not of infinite length, only approximates to a cylindrical shape in *Loligo* and *Sepia*, and the mantle muscle may not all be involved in the production of each pressure pulse. Nevertheless, this method allows an approximate value of muscle tension to be calculated. For a maximum pressure of 180 cm. in *Sepia* of 250 g. wet weight a muscle tension of 840 g./cm.² is required and for 300 cm. from a *Loligo* of 350 g. a tension of 1500 g./cm.². The latter is comparable to that determined for the arms of the octopus and is the same as that determined for the pallial and adductor muscles of the bivalve *Ensis* in the production of pressures of the order of 100 cm. (Trueman, 1967).

Another factor relevant to jet propulsion in the cephalopods is the speed with which the fluid emitted from the mantle cavity can reach maximum velocity. By means of stroboscopic photography Packard (1966, 1968) has determined that *Loligo* of body weights of 3 mg., 3 g. and 200 g. attain maximum velocity in < 50, 50–60 and 85–125 msec. respectively from standing starts. This is comparable to the time for maximum tension to develop in a mantle-nerve preparation of *Loligo pealii* (Young, 1938). Study of the rise in tension in the recordings presented here indicates that it rises to a maximum in 60 msec. in *Loligo* or *Eledone* and 100 msec. in *Sepia*. In recordings giving maximal pressure and tensions the leading edge of the pulses are at their steepest. In *Loligo* and *Sepia* these are almost certainly brought about by a giant-fibre response. The latter is characteristic of an all-or-nothing contraction system, the time taken for the mantle to contract being constant and independent of the degree of shortening of the muscle fibres. Close examination of Prosser & Young's (1937, Figs. 1, 4, 13) recordings of isolated giant-fibre nerve-muscle preparations of *Loligo* shows that the same time is taken for tensions of different amplitudes to develop. When small pulses are developing the pressure rise is slower than for maximal peaks (compare 1st and 3rd pressure pulses in Fig. 2*b*; the pulse widths are progressively shorter despite rising amplitude). On the evidence of *Loligo* (Young, 1938) the initial slow slope of the lower pulses would be due to the graded contraction of the mantle under control of small-diameter nerve fibres.

The observations described in this paper indicate that while respiratory movements

of the mantle generate only low pressures and probably have little effect on blood flow, the much higher pressures encountered during jet propulsion must cause a surge of blood in the vena cava similar to, but more extensive than, those described by Johansen & Martin (1962) in relation to respiration in *O. dofleini*. Such surges will tend to cause dilation in the large haemocoelic channels in the head which may influence the shape, and hence the focusing, of the eye as has been discussed by Boycott & Young (1956) in respect of the octopus. In the Cephalopoda such pressures must be the principal disadvantage of jet propulsion. The effect of the powerful contraction of the mantle muscles is possibly limited in extent, being buffered by the extensive coelom. This condition makes an interesting comparison with that of the Bivalvia where the coelom is small and somewhat similar high pressures are produced by the adductor and pallial muscles. In this group the pressures are utilised in burrowing (Trueman, 1967); jets from the mantle cavity displace the sand and the pressure, produced simultaneously in the body, causes blood to flow into the pedal haemocoel where it serves a locomotory function. Similar movement of the blood in the Cephalopoda would not be compatible with their high neural organization and this may have proved an important factor in relation to the evolution of an extensive coelom.

SUMMARY

1. Recordings have been made of the pressures in the mantle cavity of some coastal cephalopods, both at rest and while swimming, under conditions as near normal as possible. Pressures of up to 180 cm. of water were developed by *Sepia officinalis* (250 g. weight), 300 cm. by *Loligo vulgaris* (350 g.) 170 cm. by *Octopus vulgaris* (370 g.) and 400 cm. by *Eledone moschata* (600 g.).

2. The momentum produced by the efflux of the jet of water from the mantle cavity was recorded on an isometric myograph, attached to the head of the animal by a thread, as a tension. The swimming tensions, derived from maximum jet pressures, were in general equivalent to the body weight in *Loligo*, *Sepia* and *Eledone* but in *Octopus* never exceeded half body weight.

3. In *Octopus*, however, the arms are powerfully developed and, using five arms for attachment to the side of the tank, they can exert holding tensions of up to 100 times their body weight. In an *Octopus* of 1 g. body weight this is equivalent to a tension of 2 kg./cm.² in the longitudinal muscle at the base of the arms.

4. Comparisons of the tensions and pressures obtained in simultaneous recordings during jet swimming showed, that, with the exception of *Octopus*, the tension developed is generally equal to twice the cross sectional area of the jet multiplied by the pressure.

5. The theoretical maximal velocity for a single jet cycle in *Loligo* and *Eledone* was in accord with observed velocities and the much lower theoretical velocity of *Octopus* is discussed.

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